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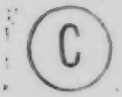

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Abstract

A series of experiments was performed to determine the effectiveness of long-term selection for increased 21- and 42-day body weight, and its influence on growth rate, feed efficiency and carcass composition in several lines of mice. These inbred and non-inbred lines of mice were also examined under the influence of cold temperature, to assess the response in growth and reproductive performance of pureline and crossline mice to a cold environment. Also, to summarize the usefulness of these experiments in planning and interpreting selection studies with domestic livestock, correlated responses to selection are examined from a biological rather than from a purely biometrical point of view.

1. Characterization was made of some of the physiological effects of selection for growth rate in mice. Growth rate and body composition were studied in three lines of mice; one selected for high 6-week body weight from a large population size (HL); one selected for high 6-week body weight from a small population size (HS); and a random bred control (C). At 6 weeks of age, body weights were 28.0, 19.1 and 12.7 for the HL, HS and C lines. Mice were serially slaughtered at 3, 4.5, 6, 9 and 12 weeks of age and analyzed for fat, protein and ash content. At 6 weeks of age, apart from % fat in the HL line, there were few differences between the lines for the body components analyzed. Males had lower percentage body fat than females in all lines. The HL line mice rapidly became fatter with increasing body weight.
2. The nature of genetic variation in growth rate influenced by selection under *ad libitum* feeding possibly reflects differences

in the efficiency of utilization of energy for gain due to differences in body composition and differences in maintenance requirement. Body weights and feed consumption data were recorded during a 9-week period, from weaning to 12 weeks of age, in individual and group-fed mice from the HL, HS and C lines. The C line consumed significantly less feed than the selected lines, their gain in body weight was much slower ($P < .05$). Efficient conversion of feed into biomass was highest in the HL line, with no significant difference in ranking between the other lines. Thus after many generations of selection on *ad libitum* feeding, selection increased food intake and body weight. Growth efficiency (gain/feed) increased in the selected line but the composition of gain was towards an increase in the relative proportion of adipose tissue. The higher growth efficiency of the HL mice during the postweaning trial period is reflected in an increased proportion of fat deposition during this stage of development.

3. The effects of cold stress on postpartum performance was studied in a 4x4 diallel cross among lines of mice which differed in body weights relative to age, level of inbreeding and previous selection history. At birth, litter weight and percent mortality were significantly influenced by mating system and environment. Pureline litters had significantly lower litter weights ($P < .05$) and higher mortality ($P < .01$) in the cold environment than did crossline offspring. Litter size (total born) and dam parturition weight were not significantly altered by the cold environment. Covariance analysis of the biological constituents at parturition revealed that litter size was a highly significant ($P < .01$) source

of variation for litter weight, in both environments. Percent mortality was an important factor ($P < .05$) influencing litter weight in the cold environment when adjusting for litter size. Use of dam weight in the model as an additional covariate accounted for some of the variation ($P < .05$) due to percent mortality in the cold environment and for litter weight ($P < .05$) in the control environment. Dams weighing above the mean tended to have litters which survived better in the cold environment and had heavier litter weights in the control environment.

4. The effects of cold stress on preweaning performance were estimated from the offspring obtained in a 4x4 diallel cross (see #3 above). Genetic differences in progeny weaning weights (actual and adjusted for litter size) and total weaning weights were measured in both sexes for all 16 genetic sets in each environment. Actual and adjusted progeny body weights and total weaning weights (TWW) were heavier ($P < .01$) for litters raised in the control environment. Simultaneous least squares analyses of purebred and crossbred groups were made. Sex differences were highly significant in both environments for weaning weight, with males being heavier than females. Purebred lines differed considerably in progeny weaning weights. Line 512 was significantly ($P < .01$) heavier in both environments for 21-day progeny body weights (both actual and adjusted). Crossbred offspring consistently were heavier than purebreds at weaning in the cold environment. The two outbred lines 511 and 512 produced the heaviest TWW in the control environment. Lines 511 and 311 had the best TWW in the cold environment.

Parameters estimated were average direct (l_i) and average maternal (m_j) genetic effects, general combining ability (g_{ij}), specific combining ability (c_{ij}), heterosis (h_{ij}) and reciprocal (r_{ij}) effects in each environment. For 3-week progeny weight, ranking of parental lines in the control environment (unadjusted) was 512 > 311 > 312 > 511; adjusted were 512 > 312 > 311 > 511; rankings were 511 > 311 > 512 > 312 for m_j and 512 > 312 > 511 > 311 for g_{ij}. Purebred effects were significant in favor of line 512, illustrating its positive response to selection for higher weaning weight.

Ranking of parental lines in the cold environment was similar for both actual and adjusted weaning weights, 512 > 511 > 311 > 312. Line rankings for offspring raised in the cold environment were as follows: 311 > 512 > 511 > 312 for m_j and 511 > 312 > 512 > 311 for g_{ij}.

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I wish to dedicate this thesis in memory of my parents, Helen and Clifford Bailey; and to my wife Kathleen, for her moral support, encouragement and understanding throughout this thesis.

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I. INTRODUCTION

Growth, according to Widdowson (1968), has one simple definition - an increase in size; but an increase in size has many implications. The word 'growth' can be used to describe an increase in mass (weight) per unit time or to describe a change in form and composition resulting from differential growth of the component parts of the body (Fowler, 1958). For purposes of the thesis, growth is defined in biological terms, specifically the growth of the major tissues of the carcass which are muscle, fat and bone.

When growth is more, or is less rapid in one part of an organism than another, change in shape will usually be the result. This need not always be true, for example, growth at only the surface of a sphere, can leave it a sphere. Nevertheless, the importance of differential growth in contributing to the final form of an animal is evident from any comparison of embryo and adult. Each species has characteristic proportions and thus, the relative growth of its different parts must be co-ordinated. Initially, organs that are growing with exceptional rapidity may appear to be immune from the controls affecting the growth of the rest of the animal, but often one finds that the two are related in an essentially simple way. If y is the dimension of a part and x of the whole then $y = ax^b$, where a and b are constants. If b is 1 then y and x are growing without change in relative size. If b is greater than 1, y is growing disproportionately fast, if less than 1, disproportionately slowly, relative to the whole animal. The equation may be written as $\log y = \log a + b \log x$ (Huxley, 1932).

Growth relationships which follow this formula are allometric. Growth is, however, far from universal and where the allometric formula does apply it may do so only for some part of the time during which x and y are growing. Many species have characteristic ranges of definitive individual size and most show a decline in relative growth rate in the later period of their lives.

In practice, it is easier to interfere with growth experimentally than to elucidate how, in nature, the many factors are actually involved. Overall, there is a genetic control most easily appreciated as such by considering the differences between large and small breeds (biological types) of animals.

The value of animals bred for meat production is influenced by their growth rate, growth efficiency and carcass quality. If animals are selected for rapid growth, it follows that they must do so by consuming more feed, or by utilizing their feed more efficiently, or by some combination of the two. As Yuksel (1979) has shown for a variety of species, both voluntary feed intake and efficiency of conversion change as positive correlated responses to selection for growth. Growth rate is most important to the economy of meat production because feed costs and most of the fixed costs decrease with increasing growth rate. As weight increases storage of fat must be kept to a minimum, otherwise it will negatively influence efficiency of growth and the price per kilogram of the product. The combination of a high growth rate and a limited fat storage can be seen in the first part of a growth curve, with optimum slaughter near the inflexion point. This is the point of the growth curve where the increasing growth rate moderates to a decreased growth rate. Brody

(1945) reported that the inflexion point for laboratory and farm animals occurs when about 30 percent of mature weight is reached.

Growth rate can be increased by improving the genotypic value for growth through both selection and crossbreeding. Heterosis for postweaning growth (Fredeen, 1957; Skarman, 1965 for pigs and Gregory *et al.*, 1966; Gall and Kyle, 1968; Cundiff *et al.*, 1981 for beef cattle) cannot be ignored in practical livestock operations. Thus breeding systems based on the crosses of lines intensely selected for growth rate would appear to be the optimum strategy for livestock improvement.

Animal breeders are interested in maximizing net economic performance in their breeding programs. Characteristics that are of importance to animal production include reproduction, survival, and postweaning growth and carcass quality. However, it is difficult to select for reproductive traits because reproduction is complex and hard to define. It is also difficult to select for carcass quality because of the problems in evaluating live animals. Thus, because of ease of measurement, research emphasis has been on selection for rapid growth rate. Long-term selection for growth rate has allowed researchers to examine to what extent selection for one trait (i.e., growth rate) may have influenced performance in these other traits. Unfortunately, the consequences of selection for growth rate on body composition, on feed conversion efficiency and on reproduction rate have not been clearly defined. Further, the consequences of selection under one environment and its implications to performance in other environments, has received scant attention. The purpose of the experiments described in this thesis was to examine some of these issues.

II. GENERAL BACKGROUND OF EXPERIMENTAL MOUSE POPULATIONS

Sources of Mouse Lines

The mouse colony was originally started in 1961 by Drs. J. A. Newman and H. T. Fredeen, working at Agriculture Canada's Research Station, Lacombe, Alberta.

The Lacombe Research Station obtained four highly inbred strains of mice from Jackson Laboratories, Bar Harbour, Maine in August 1961. The four strains, C57-Br/cd, A/J, DBA/1 and RFM, were then intercrossed to produce a new strain designated Strain 3 (Newman, 1981).

Four non-inbred strains of mice were imported from the Institute of Animal Genetics, Edinburgh, Scotland, in September 1961. The four non-inbred strains, Q, NB, JH and XL, were intercrossed to produce a new strain designated Strain 5.

Inbred mice	Non-inbred mice
4 lines intercrossed	4 lines intercrossed
↓	↓
Strain 3	Strain 5

The duration of selection in terms of the number of generations was variable between lines and, in 1979, selection was relaxed in all lines due to budgetary restraints. Thus the lines in this study were maintained at the levels achieved prior to relaxation of selection (Sumner, 1981) and represented approximately 70 generations from foundation.

Specific Lines Utilized

The lines chosen for use in this study were from genetically plateaued populations resulting from relaxation of selection, however, the lines had plateaued at very different levels. The lines used in the measurement of growth rate, growth efficiency and carcass composition were as follows: HL and HS mice - selected for high (H) individual 6-week body weight and from large (L) or small (S) population sizes, respectively. An unselected line was included as a control (C) (Fredeen, 1981). The lines used in the diallel cross experiments included lines 311, 312, 511 and 512. These four experimental lines differed in that 311 (HS) and 312 (HL) were from a highly inbred stock population, whereas 511 and 512 were derived from noninbred lines.

Selection pressure	Population size*	
	Small (S)	Large (L)
High (H)	311, 511	312, 512
Random (R)	321, 521	322, 522

*Small population size involved 2 males and 6 females per generation.
Large population size involved 5 males and 15 females per generation.

Stock control (300) derived from inbred mice, hereafter defined as C, was based on 25 single pair matings per generation.

Samples of the lines used in these studies were transferred to the University of Alberta, Department of Animal Science facilities at 3

stages, 1981 (growth and carcass), 1982 (growth efficiency), and 1983 (diallel cross). The first transfer was approximately 70 generations from foundation and those in 1983 were approximately 6 generations further removed.

Management at The University of Alberta

Representative samples of mice from each line were kept in an environmentally controlled room. Room temperature was maintained at 21 ± 2°C with a relative humidity of 45 ± 5%.

Wire topped, polypropylene cages with deep-drawn feeders were used to house the mice. Dried pine sawdust was used as the bedding material and cages were changed once per week. A commercial feed (Olde Guilford-Breeder diet)[1] consisting of ground whole wheat, casein, dried skim milk, dehulled 50% soybean meal, fish meal, corn oil, brewers yeast, stabilized Vitamin A and D, salt and ferric citrate was provided *ad libitum*. Manufacturer's guaranteed ration to contain 19% protein, 11% fat, 52% nitrogen free extract (NFE) and a maximum of 2.5% crude fiber. Tap water was supplied *ad libitum* in 250 mL glass bottles. Lighting was on a 12-hour photoperiod.

Mice within each line were single pair mated in individual cages at 8-9 weeks of age, with the avoidance of full sib matings. Males were removed from the cages 17 days after pairing. Pregnant females were examined twice daily to determine parturition. No attempt was made to standardize litter size. Litter size, weight, sex and dam

---

[1]Olde Guilford 911R, manufactured by the Emory Morse Co., Box 313, Guilford, Conn. U.S.A.

weight were recorded at parturition and individual weights were taken at 21 days of age (weaning). Only first parity litters were used in these studies.

III. GROWTH RATE AND BODY COMPOSITION OF MICE FROM 3 TO 12 WEEKS OF AGE

A. Introduction

Knowledge of the long-term effects of selection for economically important traits and of the causes of selection limits are important in the future planning of livestock improvement programs that will meet both short- and long-term objectives. Due to the costs and particularly the time involved, genetic limits to directional selection can rarely if ever be studied in livestock species. Therefore, results of laboratory animal experiments represent the primary source of evidence on selection limits in animal populations (Al-Murrani, 1974). Fortunately, as Berg and Butterfield (1976), and Barria and Bradford (1981) point out, the inheritance of basic processes such as growth and reproduction appear to be quite similar across species of mammals. Thus laboratory animals can be used to establish principles that are generally applicable to livestock species.

The majority of quantitative studies of carcass composition (in particular, fat deposition) in laboratory animals have been conducted with lines of mice which have been selected for increased or decreased weight at a fixed age or for a fast or slow rate of growth over a defined time period (Roberts, 1966; 1979). The changes that occur in traits not directly selected are called *correlated responses*. It was these responses in measures of fat and protein (nitrogen) percentages that were of interest in this study.

B. Materials and Methods

Mice Lines

The lines of mice used in this study, listed in Table III.1, were transferred to the University of Alberta, Department of Animal Science facilities in 1981. As noted in the description of the background breeding program at Lacombe, the HL line (312) and the HS line (311) had been selected for rapid postweaning gain (42-day body weight minus 21-day body weight). Two non-selected lines, one from a large population size (RL = 322), and the other from a small population size (RS = 321), were also included in this experiment along with the random-bred stock control (line 300). The formation of the stock populations and management of the colony were previously described in Chapter II, "Background History of Mouse Colony".

Experimental Design

Seventeen days after mating, males were removed and females placed in individual cages. Standardization of litter size at birth was not performed to permit full expression of the female's postpartum performance. Mice were identified by ear-notching at 12 days of age and weaned at 21 days. Mice of like sex, postnatal litter and line were randomly assigned to cages in groups of four. Dams were fed Olde Guilford 911R mouse ration *ad libitum* during lactation; after weaning the progeny were fed the same ration *ad libitum*. All mice were individually weighed at 21, 31, 42, 63 and 84 days of age.

C. Sampling of Mice for Chemical Analysis

A total of two hundred and sixty-five mice were randomly selected from five lines, for body chemical composition analysis at 3, 4.5, 6,

Table III.1. History of mouse lines used in present study, outlining number of generations, population size/generation (♂♀) and type of selection.

Line	Generation	Population Size	Selection Pressure
C	78	Large (25:25)	Random
HL	69	Large (5:15)	High
HS	53	Small (2:6)	High
RL	9	Large (5:15)	Random
RS	8	Small (2:6)	Random

9 and 12 weeks of age. The number of mice sampled from each age-line subclass shown in Table III.2. Mice chosen for body composition analysis had their feed removed 6 h prior to killing. Killing was accomplished by cerebral dislocation. The mice were stored in labelled plastic bags at -20°C pending analysis.

D. Chemical Analysis

Sibbald and Fortin (1981) proposed a simple and efficient method of whole animal sample preparation for adequate subsampling by using a steam autoclaving technique. For the present study a modified variation of their technique was used. Whole mice were placed in 600 ml beakers and 10 ml of water were added to each sample then autoclaved at 110°C for 14 h in a Sylron/Barnstead Steam Sterilizer 3122.[2] Sterilization and processing was achieved while maintaining 15 psi pressure in both the jacket and chamber. The beaker and contents were then transferred to a Polytron PCU-2 homogenizer[3] where the contents were reduced to the consistency of a puree in 2 min. The homogenous samples were frozen (-20°C) and placed in a freeze-drier for 5 days (maximum shelf temperature -20°C). The freeze-dried weight was taken before grinding the sample in a Micro-Mill electric grinder.

The water content of each carcass was calculated from the difference in body weight before and after freeze-drying and corrected for any residual moisture which was determined by heating a 1 g sub-sample of the freeze-dried material at 105°C for 12 h.

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[2]Barnstead Company, Boston, Mass., U.S.A.

[3]Brinkman Instruments, Rexdale, Ontario, Canada.

Table III.2. Sample size allocation for body composition analyses for each line-age subgroup.

Line	Age (weeks)					
	3	4.5	6	9	12	Total
HL	10	9	9	8	8	44
HS	7	10	9	8	9	43
C	14	15	14	14	11	68
RL	14	14	12	15	14	69
RS	10	7	7	8	9	41
Total	55	55	51	53	55	265

Duplicate freeze-dried tissue samples were analyzed to extract lipids with nitrogen; these were determined on the lipid free residue by means of the micro-Kjeldahl auto-analyzer. Ash was determined as the residue from subsamples of the freeze-dried extract after ashing for 2 h at 600°C.

The method of lipid determination was considered the most crucial and therefore specific attention was given to choice of method. The method chosen was as follows. Solvent extraction of the duplicate freeze-dried tissue was obtained using petroleum ethers in conjunction with the Goldfish apparatus[4] according to AOAC (1980) method. The procedure involved extracting a 1 g sample for 4 h with petroleum ether (BP 30-60°C), collecting the extract in a tared beaker, evaporating the solvent and weighing the residue.

E. Statistical Analysis

Growth was expressed in terms of grams of body weight gain during the 9-week period immediately following weaning at 3 weeks of age. The data were summarized into time intervals of 3-4.5, 4.5-6, 6-9, 9-12 and 3-12 weeks of age to represent most rapid early postweaning gain (time intervals 1 and 2), late postweaning gain (time intervals 3 and 4) and total postweaning gain to 12 weeks of age, respectively. A 3 x 2 x 5 multiway design was employed. The analysis of variance model contained the fixed effects of line, sex, age (discrete value) plus all interactions and a random error term.

$$Y_{ijkl} = u + L_i + S_j + (LS)_{ij} + A_k + (LA)_{ik} + (SA)_{jk} + (LSA)_{ijk} + e_{ijkl}$$

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[4] Labconco, Kansas City, Mo., U.S.A.

where Y_{ijkl} = an observation on the l^{th} mouse in the ijk^{th} subclass.

u = overall mean

L_i = effect of the i^{th} line (i = 1, 2, 3)

S_j = effect of the j^{th} sex (j = 1, 2)

A_k = effect of the k^{th} age group (k = 1, 2, 3, 4, 5)

$(LS)_{ij}$, $(LA)_{ik}$, $(SA)_{jk}$, $(LSA)_{ijk}$ are the interactions among the main effects

e_{ijkl} = random error term

The data were analyzed by Harvey's (1975) least-squares procedure for unequal subclass numbers using Alan's program (Alan's Program, University of Alberta, 1978).

F. Results

Growth Rate

The line rankings for 21-day body weight were HL > RL = HS > RS = C with $P < .05$ for all HL comparisons but not for RL and HS vs. RS and C. As growth proceeded, the lines diverged in weight with this progressive divergence resulting in 12-week weights for the HL line 150% of C ($P < .01$) but the RL line (102% of C) and RS (98% of C) were essentially identical with the control (Figure III.1). Sex differences in weight (males > females) were significant at all ages, increased with increasing time (A x S interaction, $P < .01$) but were not influenced by line (Table III.3).

Body Composition

The data of Table III.3 also document the significant line, sex and age differences in body composition. The age trends in body fat (Figure III.2) were substantial, HL increasing progressively from 38 to 45% from 3 to 12 weeks of age, while HS and C lines both had weights approximately 31% fat at 3 weeks which decreased to 27.5% by week 12. Trends for the other lines are not illustrated as they were essentially equivalent in fat (and not significantly different from) to the C line at all ages. Because of this progressive divergence (e.g., HL vs. C), the age x line interactions were significant ($P < .01$).

Sex differences in fat were also significant (Table III.3) and these differences (generally females > males, Table III.4) varied among lines and increased with increasing age thus giving significant ($P < .01$) interactions of A x S, S x L, and A x L x S (Table III.3).

Percentage protein was inversely related with percentage fat, an inevitable consequence of the statistical interdependence of the percentages for tissue components in the carcass imposed by the fact that their sum approximates 100%. Thus, the levels of significance for percentage protein (Table III.3) were in full agreement with those obtained for fat.

Ash content differed among lines ($P < .01$) with some line tending to increase ($P < .05$) as age increased. This increase was not uniform among lines thus producing a significant ($P < .05$) A x L interaction (Table III.3).

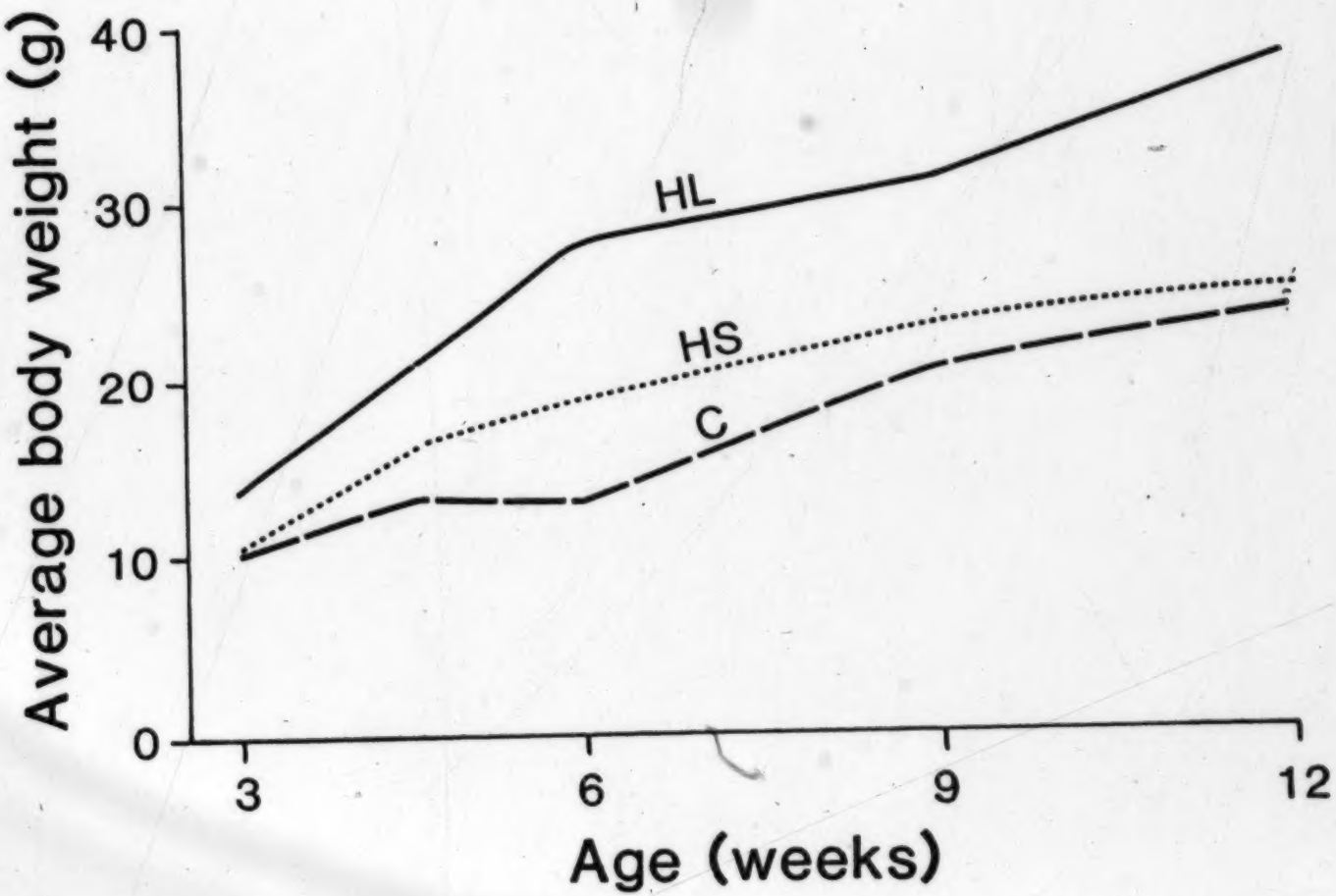


Fig. III.1 Average body weights of each age by line subclass, plotted against age.

Table III.3. Mean squares for body weight and carcass composition at five slaughter ages.

Source	df	Mean squares			
		Body wt. (g)	% fat	% protein	% ash
Line (L)	2	958.98**	2822.23**	2246.11**	73.39**
Sex (S)	1	200.83**	477.76**	380.26*	1.31
Line x Sex (LS)	2	8.08	80.18*	33.29*	0.70
Age (A)	4	1168.24**	84.06**	118.75**	7.02*
Age x Line (AL)	8	36.90**	124.41**	71.92**	4.64*
Age x Sex (AS)	4	23.27**	147.53**	84.36**	2.93
LSA	8	11.78**	21.08**	32.50**	1.38
Error	118	6.36	60.43	42.91	1.07
Total	147	54.26	114.60	87.00	2.65

**P < .001.

*P < .05.

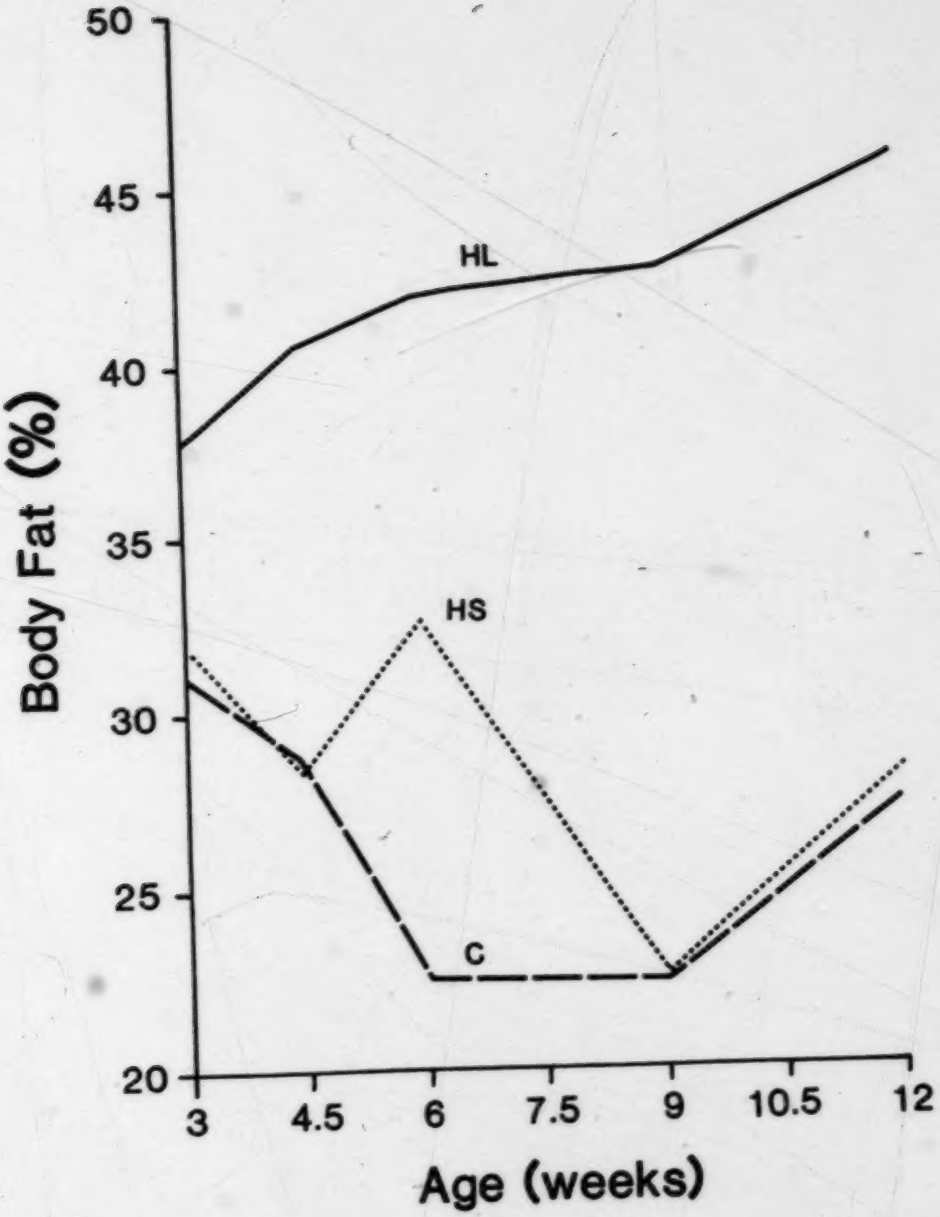


Fig. III. 2. Percent body fat of mice at various ages

Table III.4. Least-squares means (± S.E.) of body composition (%) of mice from 3 to 12 weeks of age.

Age	Line	% fat		% protein		% ash	
		1*	2**	1	2	1	2
3	HL	39.0 ± 4.5	37.0 ± 3.2	49.1 ± 3.8	48.5 ± 2.7	7.7 ± 0.6	7.8 ± 0.4
	HS	32.0 ± 3.5	32.0 ± 4.5	50.3 ± 3.0	49.8 ± 3.8	9.5 ± 0.5	9.3 ± 0.6
	C	31.1 ± 2.8	31.0 ± 3.5	58.4 ± 2.3	58.7 ± 2.9	8.2 ± 0.4	8.8 ± 0.5
4.5	HL	32.6 ± 3.9	48.7 ± 3.9	50.0 ± 3.3	38.3 ± 3.3	4.4 ± 0.5	6.6 ± 0.5
	HS	26.0 ± 3.9	30.5 ± 3.9	55.1 ± 3.2	55.5 ± 3.3	9.5 ± 0.5	9.2 ± 0.5
	C	21.5 ± 2.6	35.8 ± 3.9	63.3 ± 2.2	48.6 ± 3.3	9.1 ± 0.3	7.5 ± 0.5
6	HL	38.7 ± 3.9	45.1 ± 3.5	41.9 ± 3.3	41.6 ± 2.9	7.0 ± 0.5	6.7 ± 0.5
	HS	30.5 ± 3.5	34.7 ± 3.9	55.4 ± 2.9	51.2 ± 3.3	9.0 ± 0.5	8.4 ± 0.5
	C	21.2 ± 2.8	23.8 ± 3.9	55.4 ± 2.3	54.3 ± 3.3	9.4 ± 0.4	10.5 ± 0.5
9	HL	39.0 ± 4.5	46.3 ± 3.2	47.8 ± 3.8	40.7 ± 2.7	7.9 ± 0.6	7.0 ± 0.4
	HS	23.6 ± 3.5	21.2 ± 5.5	62.6 ± 2.9	58.4 ± 4.6	9.8 ± 0.5	11.3 ± 0.7
	C	20.4 ± 2.6	24.4 ± 3.2	63.1 ± 2.2	58.3 ± 2.7	10.5 ± 0.3	11.3 ± 0.4
12	HL	43.1 ± 5.5	48.4 ± 4.5	39.0 ± 4.6	32.8 ± 3.8	6.1 ± 0.7	7.3 ± 0.6
	HS	29.6 ± 3.5	26.9 ± 3.9	53.7 ± 2.9	55.0 ± 3.3	9.4 ± 0.5	10.8 ± 0.5
	C	26.9 ± 2.8	27.7 ± 3.2	57.1 ± 2.3	54.3 ± 2.7	9.8 ± 0.4	10.3 ± 0.4

*Males.

**Females.

Detailed evaluation of the line, age, and sex differences (Table III.4) clarified the nature of the interactions among these effects. Males of the HL line had their lowest fat content (32.6 ± 3.9%) at 4.5 weeks of age, the highest (43.1 ± 5.5%) at 12 weeks, and intermediate fat content (39%) at all other ages. Females of this line followed a different pattern, being lowest in fat (37.0 ± 3.2%) at 3 weeks and above 45% at all other ages. Males of the HS and C line had their highest fat content at 3 weeks and the lowest values at 9 weeks. Females of these lines also had the lowest values at 9 weeks but the highest values were recorded at 6 weeks for the HS line (34.7 ± 3.9) and at 4.5 weeks for the C line (35.8 ± 3.9%) as shown in Figure III.2, the HS line was identical in fat content to the C line except for the sharp divergence at ages 6 and 9 weeks. That the divergence characterized both sexes of these lines is clearly documented by the data of Table III.4.

G. Discussion

Several authors (McCarthy and Doolittle; 1977, and McCarthy and Bakker, 1979) have reported positive correlated responses in total fat in lines selected for increased growth rate. Other researchers have reported large positive divergences in skeletal dimensions (Hooper, 1977), muscle weights (Byrne, Hopper and McCarthy, 1973), and weights of fat depots (Allen and McCarthy, 1980) in strains defined as "Large" and "Small" developed by divergent selection. These observations suggest that the main effects of selection for increased growth rate (e.g. body weight) is to speed up the normal processes of cellular growth, i.e. to accelerate the processes of cellular hypertrophy and

hyperplasia. The majority of reports (Fowler, 1958; Clarke, 1969; Timon and Eisen, 1970; Hayes and McCarthy, 1976; Eisen *et al.*, 1977; Hetzel, 1978; Allen and McCarthy, 1980; McPhee *et al.*, 1980) have indicated that at equal ages, lines selected for high body weight tend to be fatter as compared with unselected lines or control lines.

Age at the time of selection appears to play an important role in the correlated changes in adipose tissue content. For example, the results of several mouse selection studies in which fat was measured over a range of ages (Hull, 1960; Hayes and McCarthy 1976; McPhee and Neill, 1976) have indicated that the rate of fat deposition (measured in terms of fat content at a constant weight basis) increases after the age at which selection occurs. Thus, lines selected at a young age for rapid growth will be fatter at later ages than an unselected (slower growing) population and also fatter than lines selected for rapid growth at a later age. This is not particularly surprising since the typical pattern of body development (Berg and Walters, 1983) involves an increase in adipose tissue content as the animal matures (i.e., becomes older and heavier). Hence, lines characterized by different growth rates (curves) would be expected to differ in proportions of the major body tissues.

The results obtained for the HL line in the present study were in general agreement with the concepts advanced in these referenced reports. Selection of the line for rapid growth prior to 6 weeks of age produced a strain that was both heavier (150%) and fatter (160%) than the control population at 12 weeks of age. Thus, whether by virtue of a proportionately larger daily feed intake and/or a proportionate change in the nature of physiological/metabolic

processes, the HL line tended to store more feed energy as fat than the control. Hayes and McCarthy (1976) suggested that mice selected for increased weight at an older age would consume more food and divert less metabolizable energy to fat production at younger ages or up to the age of selection. Using that same analogy, selection for low body weight should favor the fattest animals of all. However, Malik (1984) reported that in most experimental results reported in the literature, selection has been shown to produce lean mice by reducing appetite.

However, when one looks at the 'relative rate' of fat development in selected lines, the responses appear more complicated. In mice selected for high body weight, and where the development of fat has been measured over a range of ages, there has been a consistent change in the relative rate of fat deposition (i.e. in the regression of log fat weight on log body weight). For example, Hayes and McCarthy (1976), McPhee and Neill (1976) and Eisen, Bakker and Nagai (1977) all found an increase in the relative rate of fat deposition in mice selected for large body weight vs. control mice. Hayes and McCarthy (1976) and Allen and McCarthy (1980) have also found a reduction in the relative rate of fat deposition in small lines.

In the present study, the HL line was fatter at all ages than either the HS or C lines but the divergence increased with advancing age. This divergence reflected both the increase in the percentage of carcass fat of the HL line and the reasonably progressive reduction of body fat in the HS and C lines (Figure III.2).

The pre-evaluation selection history of these lines was based on body weight at 42 days of age. The age at selection may have conditioned the rate of fat deposition illustrated in Figure III.2 and

can be inferred from other experimental results (Hayes and McCarthy, 1976; McCarthy and Doolittle, 1977; and Sharp *et al*. 1984). For example, the above reported results were comparable to our lines (HL and C) when selected at approximately the same age; while Hull (1960) selecting for 21-day body weight found fat deposition at an even steeper rate of increase.

Another factor which may have contributed to the line differences in both growth rate and tissue composition is inbreeding. Inbreeding depression, the decline in performance associated with increased inbreeding, has been well documented (Bowman and Falconer, 1960; White *et. al.*, 1968; Eisen, 1973; Falconer, 1981). High inbreeding levels characterized all selected lines involved in this study, an inevitable consequence of the small closed populations used in all but the C line. Over time, the level of inbreeding (F_x) of all selected lines asymptoted to near unity but the rate of increase in F_x, inversely related to population size, was far faster in the HS and RS lines than in the HL and RL lines (Fredeen, 1983). Thus, chance (random drift) had greater potential to restrict genetic variability in the small (RS and HS) populations than in the large populations, thereby restricting the opportunity for effective selection and compromising the ultimate genetic limits for growth rate of these lines. While this same factor (random drift) may have influenced the total genetic variability present in the two basic strains (5 and 3), this was not because for any line differences observed in the present study since all (including the control line) evolved from the stock strain (3) which was derived from inbred strains. In this context it should be noted that the crossing of inbred lines, plateaued for growth rate through a long

history of selection for this trait, does increase genetic variability and open the door to renewed selection responses (e.g., Roberts, 1966).

Differences in F_x probably accounted for the differential responses (relative to the control) of the HL vs. HS lines. This is supported by the close correspondence of performance levels of the RL, RS, and C lines with the RL marginally superior to the RS.

The implications of this study to the livestock industry are that the relative proportions of body tissues are related to age. Protein and ash will decrease as a proportion of the carcass weight while fat increased with weight and age. The ratio of muscle:bone and fat:muscle will be of importance to the producer since these ultimately determine the acceptability of the carcass. The muscle:bone ratio is similar at a constant weight, i.e., one gets the same amount of muscle and bone on each carcass at a specific weight. The fat:muscle (protein) ratio can alter slightly depending on breed, sex and type of feed (energy content) given. The market demands a certain fat cover but a high level of muscle (meat) is necessary to obtain the optimum carcass. A possible interpretation for the changes in the relative rate of fat deposition is that it is related to selection for rate of gain (generated by the discrepancy between the energetic costs of producing muscle and fat). It is the costs of deposition, which are about 11 and 53 kJ per gram for lean and fat tissue (Webster, 1977), that are of importance to the producer.

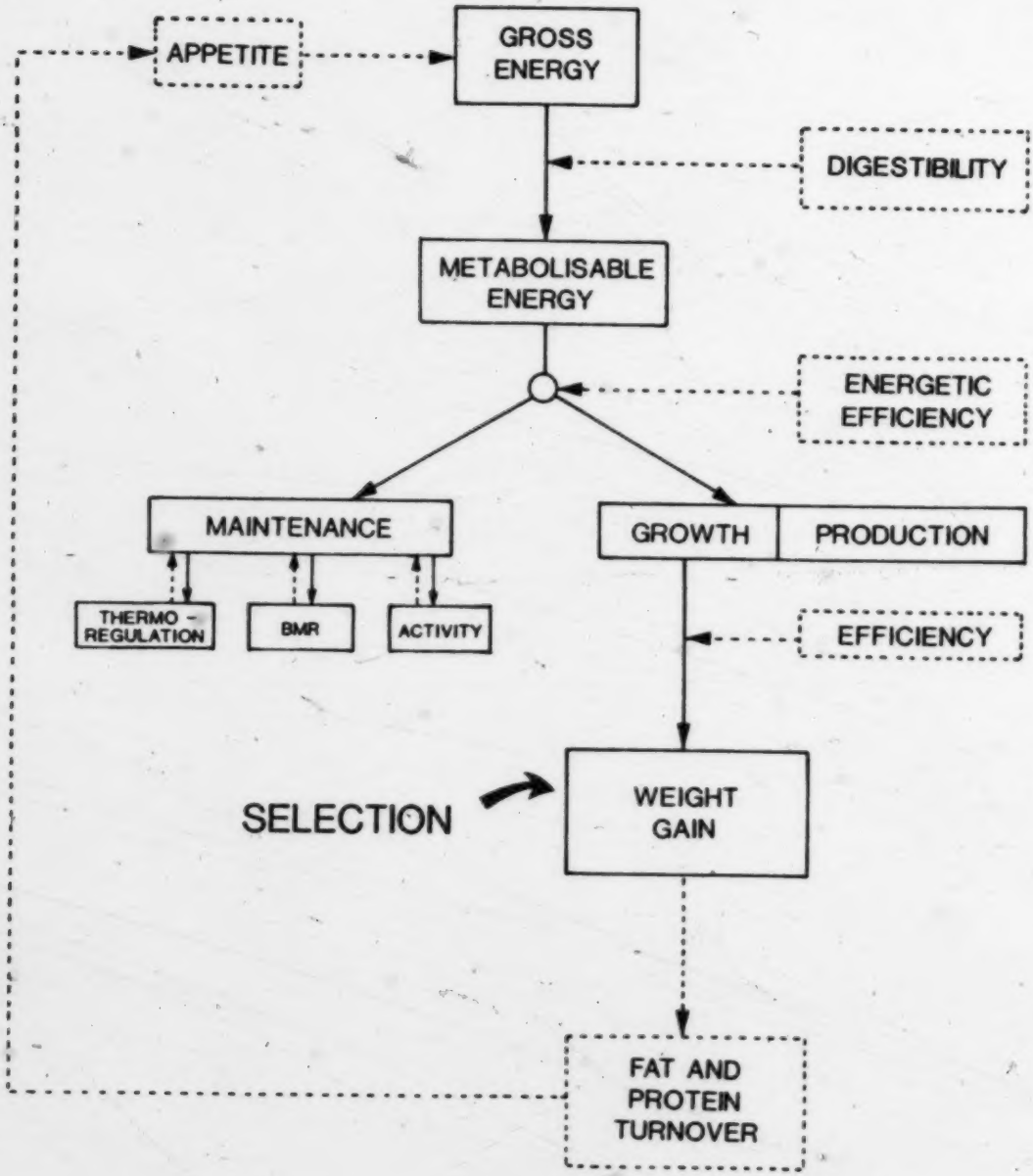
There is a related aspect of composition which follows from the responses in fatness described above, i.e., possible side-effects of selection for weight on fat distribution. Allen and McCarthy (1979) have found that different fat depots show different degrees of change

in their relative rates of growth - those depots which contribute most to gain in weight are affected most by selection. As McCarthy (1980) showed, this type of preferential correlated response in some depots results in changes in the distribution of fat even when lines are compared at the same level of fatness. Larger differences in fat distribution occur between lines when comparisons are made at fixed ages or at fixed body weights but these are generated simply as a corollary of the fact that different fat depots grow at different rates (Allen and McCarthy, 1980).

Selection for body weight or growth rate has been found by many workers to produce concomitant changes in the rate of food consumption (e.g. Fowler, 1962; Rahnefeld *et al*., 1965; Lang and Legates, 1969; Brown and Frahm, 1975; Eisen and Bandy, 1977). However, the literature on the inter-relation between changes in growth rate and feed efficiency leaves much to be desired in terms of understanding the degree to which one change precipitates the other. It is generally accepted that differences between lines in efficiency of digestion are not an important source of variation in gross efficiency (Fowler, 1962; Stainer and Mount, 1972; Puller and Webster, 1974). What then are the changes underlying increases in growth efficiency (gain/feed) at a fixed age in the HL line mice? If intense unidirectional selection for rapid growth rate in livestock species in continued, will this inevitably lead to the same end-point (i.e. increased carcass fat). Experimental evidence of partitioning of food energy between maintenance and growth; and between that available for growth between adipose and lean tissue deposition is required to explain the reasons for among-line differences in body composition (Figure III.3).

Since feed intake utilization and efficiency represent another dimension in a genetic analysis of growth rate, it was decided to measure individual feed consumption in these lines of mice. Variations in the ability of mice to consume, digest and utilize feed are all involved in growth efficiency which is discussed in Chapter IV.

Fig. III.3 Simplified Model of the Relationship Between Energy Partition and Weight Gain.



Adapted from McCarthy (1980)

IV. POSTWEANING FEED INTAKE AND EFFICIENCY OF GROWTH IN SELECTED LINES OF MICE

A. Introduction

In all classes of livestock, feed costs represent a significant part of the overall production expense. Thus, knowledge of some of the means of improving growth efficiency in meat producing animals is of major importance. Due to difficulties inherent in measuring individual feed consumption, few studies have been successfully completed in terms of direct selection for this trait (Brown and Frahm, 1975).

A high genetic correlation between postweaning gain (G) and efficiency of growth in mice has been reported by Fowler (1962), Sutherland *et al.* (1970), Bakker (1974), Yuksel *et al.* (1981), and Parker and Bhatti (1982). Because of this high correlation, most selection experiments have used growth rate as the basis for selecting for improved growth efficiency since direct measurement of the latter is difficult. Although selection for improved growth rate increases feed consumption and growth efficiency, Yuksel, (1979), Gunsett *et. al.*, (1981), and Eisen (1974) have observed that use of this selection criterion may in fact result in selection for increased appetite which may be accompanied by an undesirable increase in fatness (Hayes and McCarthy, 1976).

Variations in the ability of mice to consume, digest and utilize feed energy are all involved in growth efficiency. Growth efficiency is difficult to interpret biologically because it is the end product of complex metabolic processes and will vary with age, sex, stage of reproduction, behavior and activity, season, temperature, humidity and

possibly many other factors. For purposes of this study, growth efficiency is defined as the unit gain in body weight per unit feed consumed (gain/feed).

After reviewing possible ways that large mice can attain higher growth efficiency, Sutherland *et al.* (1974) concluded that "such increases in gross efficiency as do appear (between large and unselected lines) seem to be the result of increased capacity to ingest nutrients." Timon and Eisen (1970) had previously suggested, on the basis of covariance analysis of food consumption data from a single large line and its control, that an increase in food consumption per unit body weight was the critical change causing improvement in feed efficiency. Their conclusion applied strictly to comparisons made at the same terminal weight. Brown and Frahm (1975) performed an analysis of feed consumption data from a line selected for increased 3 to 6-week gain and concluded that while food consumption per unit body weight may not have altered, "factors in addition to increased feed consumption - perhaps physiological changes - may contribute to more efficient utilization of nutrients for body maintenance and growth."

The purpose of the present study was to examine correlated changes in postweaning growth efficiency in lines of mice which had been selected for high 42-day weights, and to compare their performance against that of non-selected randombred lines.

B. Materials and Methods

Mice Lines

The lines of mice used in this experiment were listed in Table III.1 and background information on these lines was described in Chapter II.

Feeder

A mouse feeder (Figures IV.1 and IV.2) was designed to accurately measure individual feed consumption and to minimize the problems associated with feces and urine contamination. The feeder construction consisted of a stainless steel frame and a wire mesh tunnel entrance.

The feeder was made of 26 gauge stainless steel with a 1/4 inch 20-gauge wire mesh covering the top part of the feeder (Figure IV.1). A 45° angle funnel (hopper) was used to maintain a constant source of feed and as a means of filling the internal manger. Entrance to the feeder is provided by a tunnel formed by the wire mesh (Figure IV.2). The tunnel originates at the edge of the manger and extends beyond the base of the feeder, therefore, any feed that the mouse pulls over the lip of the manger falls through the wire mesh and is collected in the base of the feeder (Figure IV.2: A-B). We found it was necessary to make the feed collector shorter than the length of the wire tunnel in order to prevent urine and feces from falling into it.

The wire forming the tunnel overlaps onto itself such that one can adjust the size of the tunnel entrance to accommodate various sizes of mice. The entrance to the feeder should not be so large that the mouse can turn around while inside the tunnel. The wire mesh aids in brushing off any feed that may be clinging to the mouse's whiskers and coat.

C. Experimental Design

Immediately after weaning (21 days) a representative sample of 6 mice was chosen from each of the 3 lines. These were weighed and separated according to sex and randomly assigned either one or three to a cage. Cages were equipped with either conventional cage-top

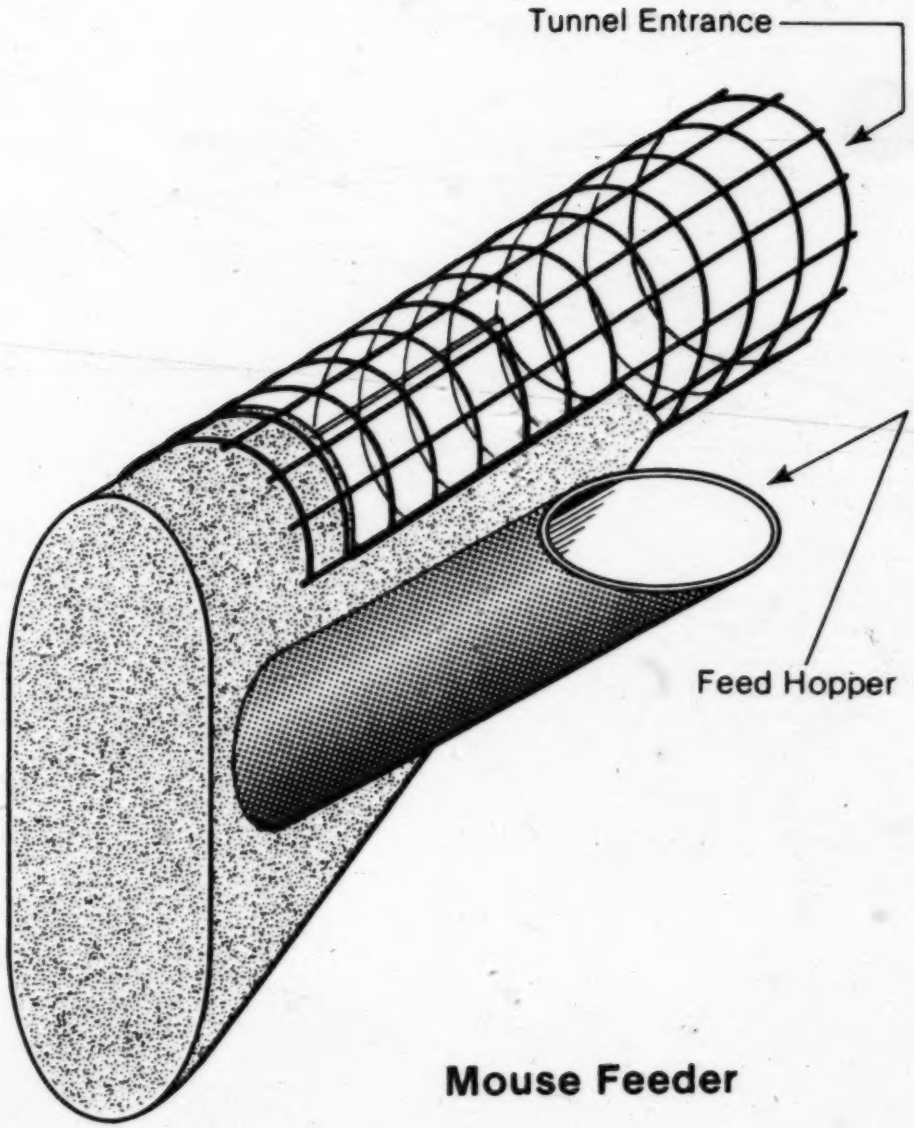


Fig. IV. 1. Schematic drawing of mouse feeder.

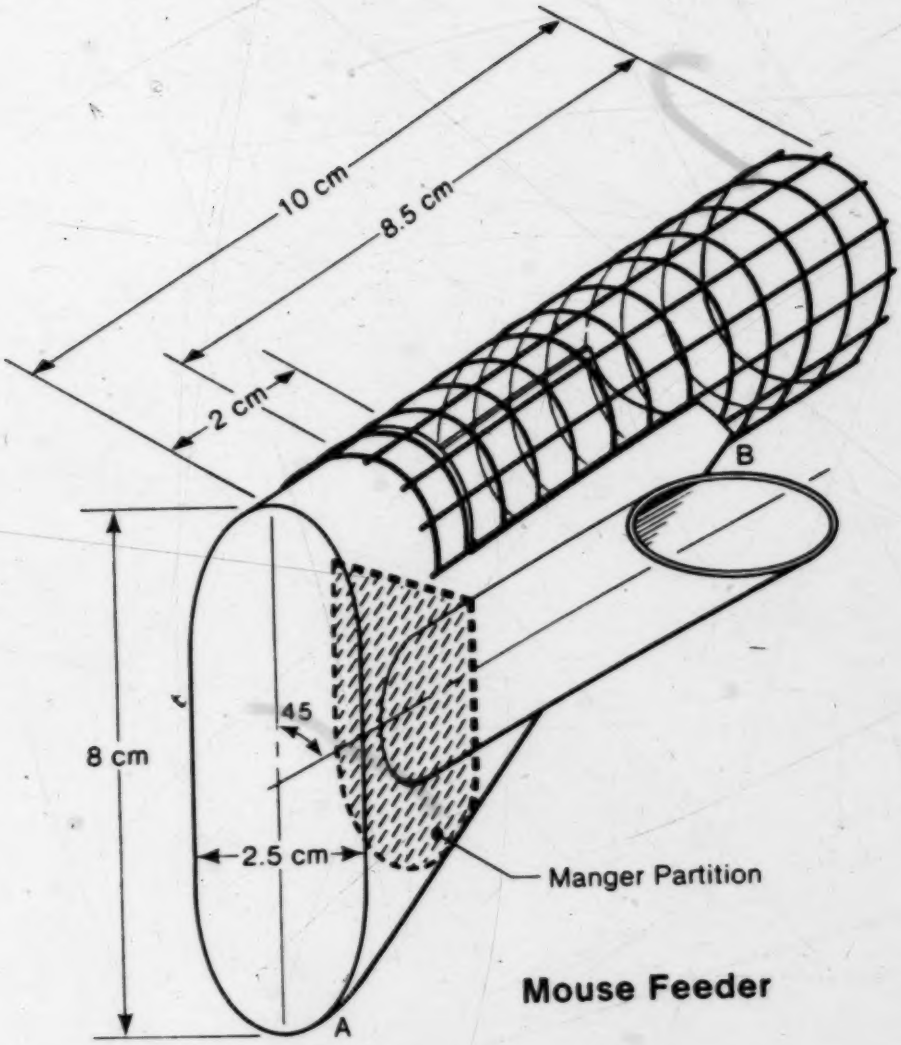


Fig. IV. 2. Dimensions of mouse feeder and showing feed collector(A - B)and manger partition.

feeders or manufactured individual feeders as previously described. When 3 mice/cage were involved, 2 individual feeders were used simultaneously. All mice were given an initial adjustment period of 3 days at the beginning of the experiment. This period was necessary to allow the mice to adapt to weaning and become accustomized to a 100% solid food diet. The laboratory was maintained at a controlled temperature of 21 ± 1°C, with a relative humidity of 45 ± 5%. A commercial feed ration (Olde Guilford 911R) and tap water were supplied *ad libitum*. Lighting was on a 12-hour photoperiod. The mice were weighed weekly from 3 to 12 weeks of age. Feed consumption data were recorded daily throughout the 9-week period. A completely randomized design was used incorporating line, sex, treatment (cage) and time.

D. Statistical Analysis

The traits analysed, using a generalized least squares procedure (Harvey, 1975), were gain, feed intake and growth efficiency. The statistical model used in the analysis included:

$$Y_{ijklm} = u + T_i + L_j + (TL)_{ij} + S_k + (TS)_{ik} + (LS)_{jk} + C_l + (TC)_{il} + (LC)_{jl} + (SC)_{kl} + (TLS)_{ijk} + (TLC)_{ijl} + (LSC)_{jkl} + (TLSC)_{ijkl} + e_{ijklm}$$

where Y_{ijklm} = an observation on the m^{th} mouse in the $ijkl^{th}$ subclass

u = overall mean

T_i = effect of i^{th} treatment (i = 1, 2)

L_j = effect of the j^{th} line (j = 1, 2, 3)

S_k = effect of the k^{th} sex (k = 1, 2)

C_l = effect of the cage density (1 or 3)

$(TL)_{ij}$, $(TS)_{ik}$, $(LS)_{jk}$, $(TC)_{il}$, $(LC)_{jl}$, $(SC)_{kl}$ $(TLS)_{ijk}$, $(TLC)_{ijl}$, $(LSC)_{jkl}$, $(TLSC)_{ijkl}$ are the interactions among the main effects

e_{ijklm} = random error term

In the analysis of feed intake, the between cages variance component was negligible compared with that between individuals. The Student-Newman-Keul multiple range test was used for comparing line differences at the 5% level (Steele and Torrie, 1980).

E. Results

Line differences in growth patterns (Figure IV.3) were closely similar to those observed in Chapter III (Figure III.1). Any differences present could have resulted from the sample size involved in the initial growth study.

Main effects of line, treatment and age were highly significant ($P < .01$) for feed intake during the 8-week study (Table IV.1). Sex effects and most interactions were non-significant. A line x age interaction ($P < .10$) approached significance, indicating that over time, the divergence in feed intake was increasing between HL and the other lines (HS and C). Average feed intake and growth efficiency (gain/feed) of the 3 lines on *ad libitum* feeding are shown in Figures IV.4 and IV.5. It is evident from these figures that the HL mice were more efficient than the other lines at any given point during the experiment.

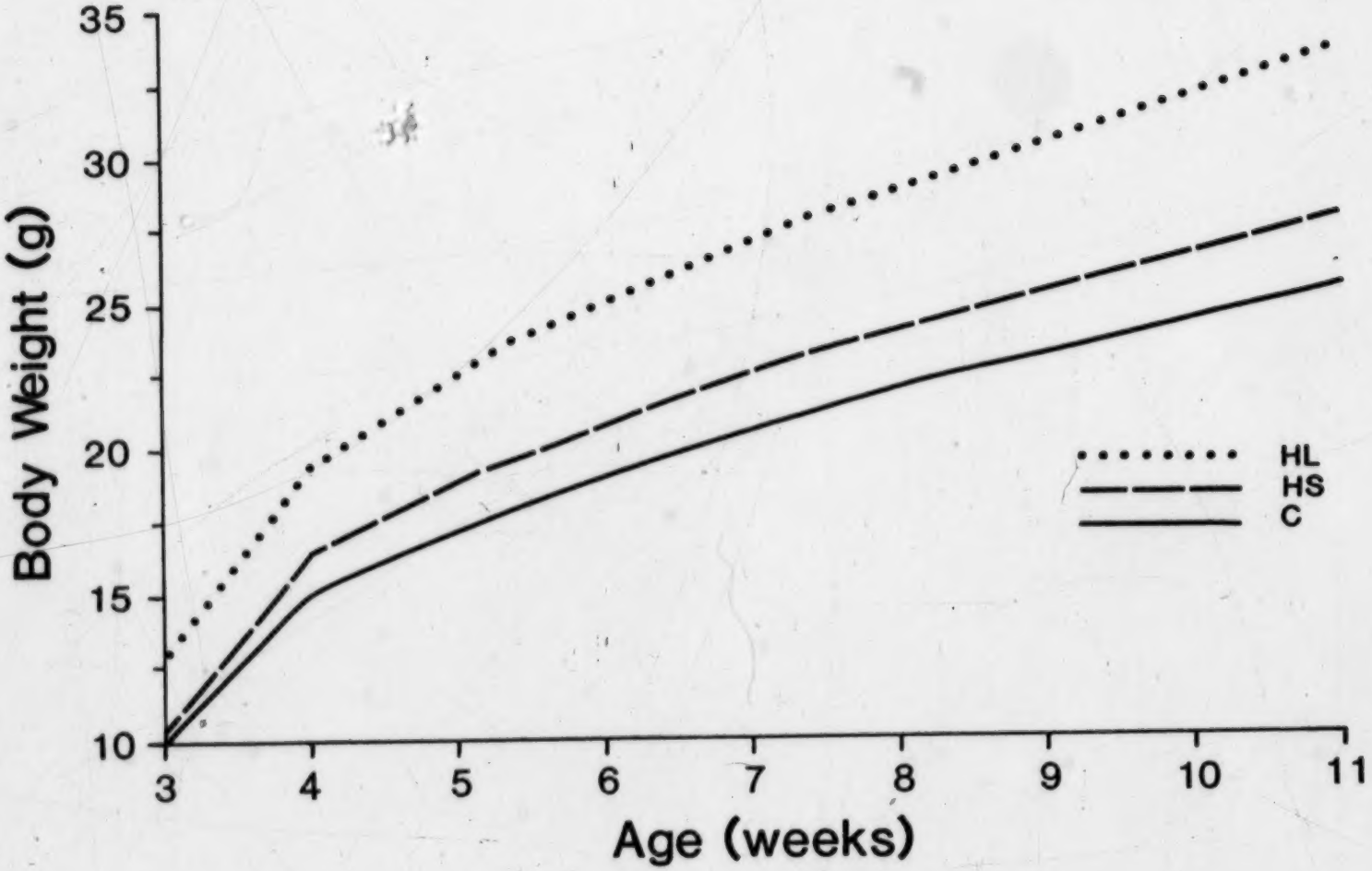


Fig. IV. 3. Body weight (g) of three lines of mice (group fed) 3 to 11 weeks age.

Table IV.1. Analysis of variance for feed intake during 8-week postweaning study.

Source	df	Mean squares
Line (L)	2	15.23**
Sex (S)	1	0.46
L x S	2	0.16
Treatment (T)	1	17.27**
L x T	2	0.63
S x T	1	0.43
L x S x T	2	1.48
Error a	60	0.64
Age (A)	7	12.13**
L x A	14	0.14†
S x A	7	0.08
L x S x A	14	0.05
T x A	7	0.09
L x T x A	14	0.06
S x T x A	7	0.09
L x S x T x A	14	0.09
Error b	420	0.09

**P < .01.

†P < .10.

[a]Error among animals.

[b]Error within animals.

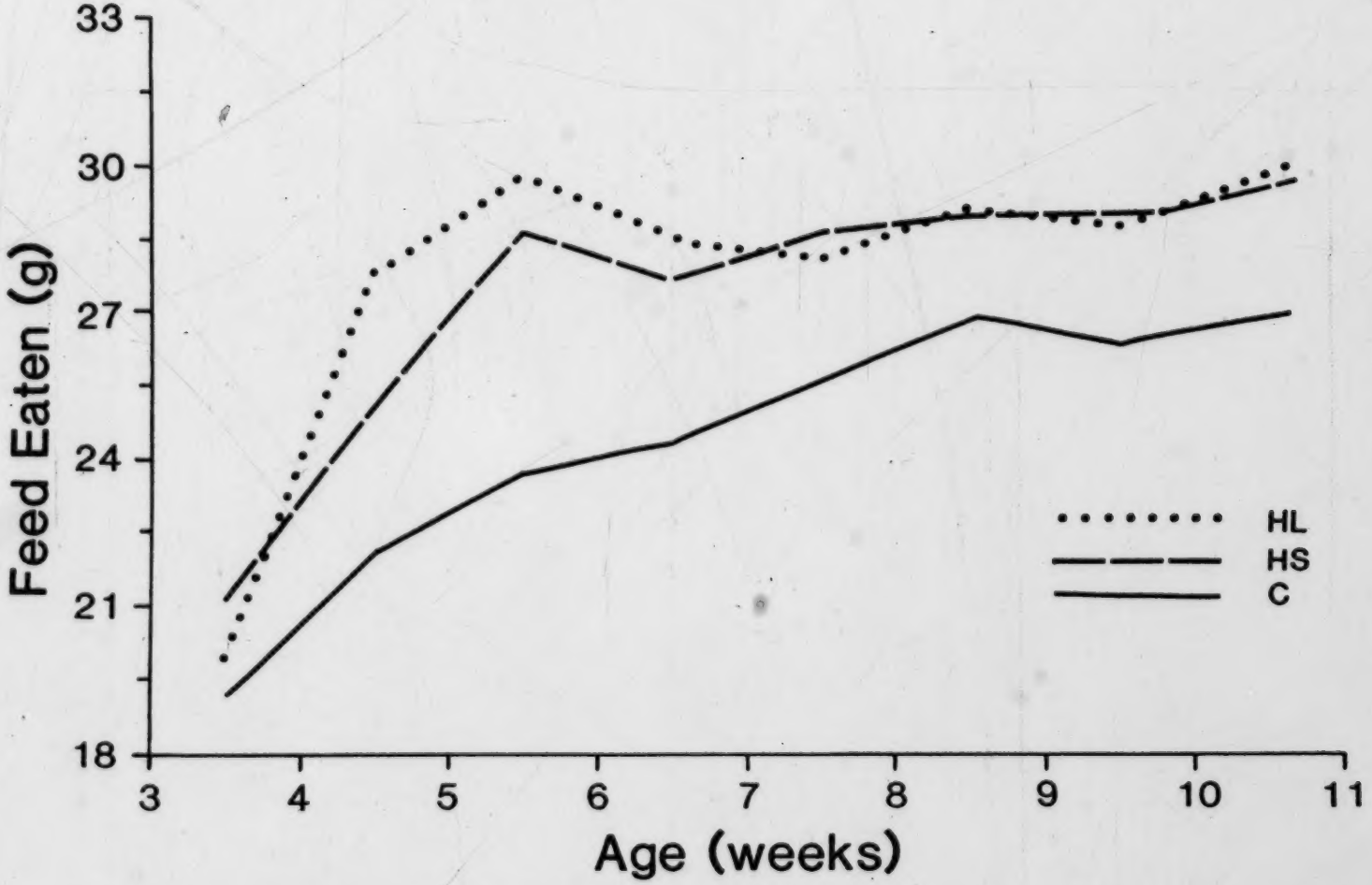


Fig. IV. 4. Least squares means of feed intake (g) per week, of the 3 lines of mice (group fed) 3 to 11 weeks of age.

Interestingly the C line consumed significantly ($P < .01$) less feed than the selected lines throughout the 8 week period. Feed intake per unit of body weight (Figure IV.5) clearly illustrated the effectiveness of selection for body weight to change the relative (feed:gain ratio) amount of feed eaten and gain measured over a fixed period.

Individual vs. group (3) caging of mice was examined with these same lines to determine if growth efficiency and growth rate were influenced by isolation. Group feeding tended to reduce daily feed intake per animal below the levels recorded for individually fed mice (Figure IV.6).

The main effects least squares means for feed intake are given in Table IV.2. The HL line mice consumed, on average, 3.93 g/animal/day. Individually-fed mice consumed approximately 0.40 g/animal/day more than group-fed mice. The largest differences in feed consumption occurred between the ages of 4 to 7 weeks (Table IV.2) after which age the differences become less as the mice reduced their intake. The peak in feed intake occurred when the mice were approximately 6 weeks of age and thereafter declined to an average level of 3.6 g/animal/day.

Least squares means and standard errors for traits measured in each of the five lines are presented in Table IV.3. There was a high degree of consistancy between males and females within each line. The HL line was 30% heavier than the C line at 12 weeks of age.

The percent changes relative to the control line are presented in Table IV.4 for feed intake and growth efficiency. Throughout the experiment, the experimental lines showed an increase in feed intake relative to the C mice. However, only the HL line was consistently more efficient in body weight gain per unit feed consumed.

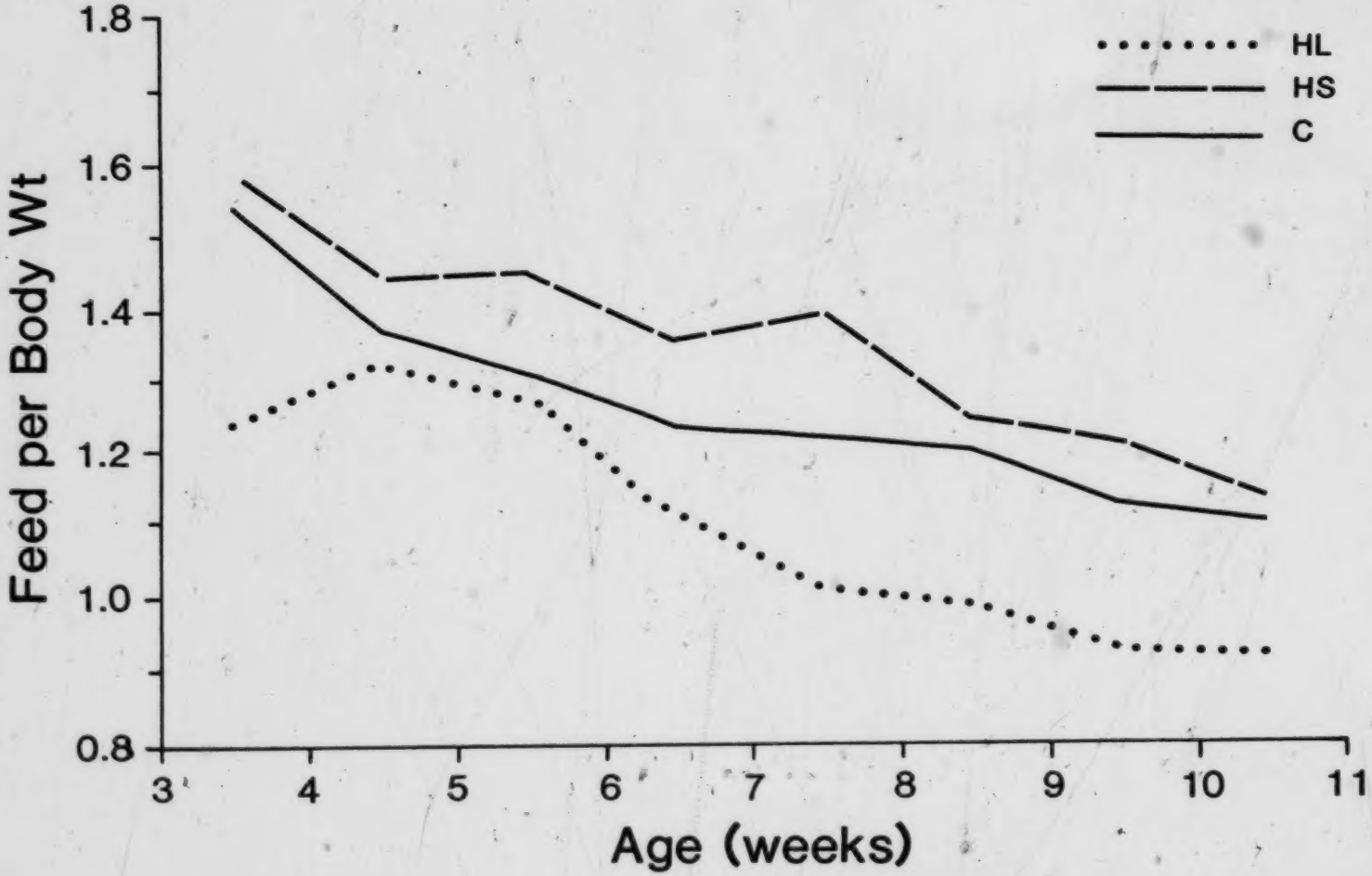


Fig. IV. 5. Mean feed intake (g) per week per unit body weight in 3 lines of mice.

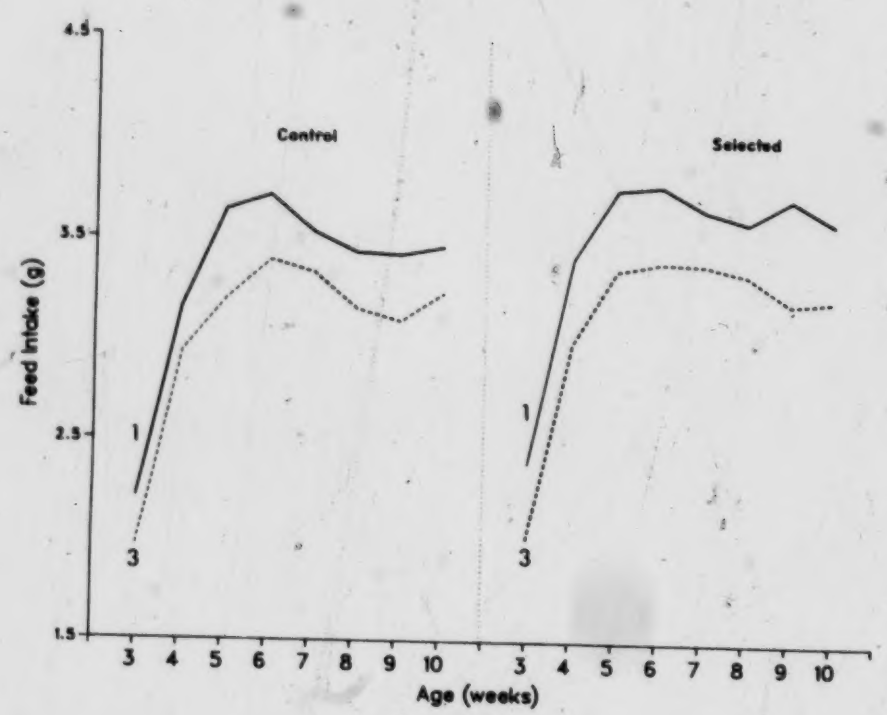


Fig. IV. 6. Average feed intake (per anim/d) of individual (1) and group-fed (3) mice from 3 to 11 weeks of age

Table IV.2. Least square means for feed intake study (main effects only).

Source	Feed intake (g/animal/d)
HL	3.93**
HS	3.39
C	3.25
Males	3.54
Females	3.50
Group feeders	3.22**
Individual feeders	3.62**
Age (wks)	
3-4	2.37
4-5	3.44
5-6	3.90
6-7	3.84
7-8	3.68
8-9	3.62
9-10	3.65
10-11	3.66

**P < .01.

Table IV.3. Least squares means and standard errors (± S.E.) of body weight, gain, feed intake (F.In.), and growth efficiency (GE) measured from 3 to 11 weeks of age in each line.

Line	3 week wt. (g)	11 week wt. (g)	Gain (g)	F.In. (g)	GE
HL	13.00a ± .57	33.31a ± .60	2.54a ± 0.05	27.71a ± .48	0.103a ± .003
HS	10.47b ± .57	27.65b ± .60	2.15b ± 0.05	27.36a ± .48	0.086b ± .003
RL	12.16ab ± .57	26.12bc ± .60	1.74c ± 0.05	27.86a ± .48	0.067c ± .003
RS	11.05b ± .57	25.12c ± .60	1.76c ± 0.05	26.17b ± .48	0.071c ± .003
C	10.25c ± .57	25.19c ± .60	1.87c ± 0.05	24.37c ± .48	0.087b ± .003

a-c Means within a column followed by different letters are significantly different ($P < .05$).

Table IV.4. Percentage changes, relative to control, in voluntary feed intake (F.In.) and growth efficiency (G.E.) from ages 3 to 11 weeks*.

	HL		HS		RL		RS	
Weeks	F.In.	GE	F.In.	GE	F.In.	GE	F.In.	GE
1	+104.40	+124.5	+110.12	+102.6	+116.97	-118.2	+108.54	-141.6
2	+125.68	+105.4	+114.07	-107.1	+117.80	-130.4	+111.09	-109.8
3	+125.84	+108.0	+120.89	-108.0	+119.14	-126.7	+104.50	100.0
4	+116.94	+116.4	+113.48	100.0	+120.01	-126.2	+107.62	100.0
5	+109.30	+125.5	+111.56	100.0	+111.77	-121.6	+112.65	-105.9
6	+108.50	+124.4	+108.07	+102.2	+112.31	-124.4	+102.67	+102.2
7	+109.18	+126.8	+110.16	+102.4	+106.69	-117.1	+107.16	100.0
8	+110.62	+123.7	+110.49	100.0	+111.96	-121.0	+103.18	+102.6

*F.In. - feed intake.

GE - growth efficiency.

F. Discussion

Roberts (1981) stated that "other things being equal", an increase in feed intake would result in a higher efficiency, at least over some range of intake. What amount is left over after maintenance requirements have been met is then available not only for thermoregulatory aspects but also for protein, fat, etc., deposition and turnover. Those animals which consume little more than their maintenance requirements will not grow as fast and will be less efficient compared to those with consumption greatly in excess of maintenance. Smaller mice have a high surface area to mass ratio and a relatively higher maintenance requirement per unit body weight. Selection for rapid growth may indirectly affect rate of protein turnover. Preistly and Robertson (1973) have suggested that protein turnover was higher in small mice and therefore would have a higher rate of protein synthesis and a more rapid rate of protein degradation. This may partially explain why large mice, with a slower rate of protein turnover, might be more efficient than small mice when compared at the same age.

The relationship between rate of feed intake and body weight in selected and unselected lines has been analysed statistically by a number of workers, but the conclusions differ. For example, Sutherland *et al*. (1970) and Timon and Eisen (1970), found that the rate of feed consumption per g body weight was significantly greater in a Large line than in an unselected one. In contrast, Stanier and Mount (1972) reported no differences in rate of food consumed between the large, unselected and small lines of mice at the same body weight and concluded that feed consumption per g body weight did not alter on selection for body weight.

Daily feed consumption curves of the lines in the present study were quite characteristic, rising almost linearly, though at different rates for each line, from weaning to approximately 6 weeks of age and thereafter slowly plateauing. In the selected lines (HL and HS), the increase in rate of feed intake was accompanied by an increase in the growth efficiency. Overall, the large mice ate more feed than small ones, but wide fluctuations in feed intake occurred among the 4 selected lines. These results differ from those obtained by Roberts (1981) in terms of feed intake immediately after weaning (Figure IV.6). He found that large and small mice consumed the same amount per unit body weight (at weaning). It is possible that the difference merely reflected the difference in the strains employed (i.e., Roberts vs. present study) since, as shown in Figure IV.4, consistent strain differences in feed intake over the 8 weeks were present. The error variation among animals was greater than the error variation between time periods for a given animal. From these results it appears that feed consumption per g body weight is less in large lines than in randomly selected and control lines at the same age, but that at the same weight, mice from different lines consume about the same amount of feed. These findings are consistant with those reported by Sutherland *et al.* (1970) and Timon and Eisen (1970).

Line differences in growth efficiency may be due to differences in the amount of energy required for: 1) maintenance, including the processes of thermoregulation, basal metabolism, muscular activity, etc., and 2) muscle and fatty tissue synthesis, deposition and degradation (turnover). Fowler (1962), reported that in terms of energy expenditure, large line mice had a lower maintenance cost than

small line mice when calculated on the basis of per g body weight expressed against age. At similar body weights, irrespective of the age, the maintenance requirements of the two lines were not different. He attributed the apparent advantage of the selected line over the control and unselected lines in gross efficiency to the increased gains in body weight associated with an increase in appetite. Canolty and Koong (1977) concluded that maintenance cost was not an important factor in influencing efficiency of energy utilization of selected mice, whereas the efficiency of energy utilization for growth was significantly increased.

McPhee *et al.* (1980) and Brown and Frahm (1975) reported an improvement in efficiency without an increase in feed intake per gram body weight. This was not the case in the present data which showed, as did Timon and Eisen's (1970), that for each additional gram of feed consumed per gram of body weight there was an associated increase in growth efficiency in the selected line.

The essential feature of the energy utilization model (Figure III.5) is that in the young growing animal, variation in growth is due primarily to variation in feed intake, and animals selected for early growth simply eat more. However, at later ages as fat accumulates, there is additional variation associated with the partitioning of feed energy between fat and protein and since fat is energetically denser than lean (Hayes and McCarthy, 1976), the leaner animals will be more efficient, and therefore grow more rapidly. It is these leaner animals that should be selected at later ages, whereas animals selected when young may simply represent those with insatiable appetities which will tend to fatness at later ages.

One obvious way to increase energy availability is to increase the rate of food consumption and this is the overriding response observed in lines selected for increased body weight. Another means of increasing efficiency, although not tested in the present study, would be to restrict the amount of feed (non-ad *libitum*) available during the postweaning growth period.

An interpretation of the results of the body composition data in light of the feed intake from these selected and control lines is needed. Possibly the differences in energetic efficiency between the lines is mainly due to an increase in the relative rate of feed intake (Metabolisable Energy per day per unit body weight) in the HL line and from a higher relative maintenance cost (Maintenance Cost per day per unit body weight) compared with the smaller animals of the randomly selected and control lines.

The weight gain and growth of the individually fed mice was below their counterparts which were group-fed (not shown). A simple answer for this occurrence is not immediate. Mice are undoubtedly sensitive to changes in environment and in groups they can utilize huddling to conserve body heat, thereby requiring less feed intake to keep warm. Mice which are singly housed would require more feed to maintain body temperature and therefore may be more active in a persistent search for companionship.

Selection for increased weight gain is not simply selection for increased appetite; in fact, changes in appetite could result from metabolic changes brought about by the specific selection criteria applied. The inter-relations between growth, feed intake and efficiency of growth in this mouse study imply that no single factor

can be adequately interpreted independently of the others. McCarthy (1980) supports the case of selection for weight since it may achieve a same endpoint as selection for efficiency, without the added expenses of feed records and extra labour.

Increased feed intake obviously increases the metabolizable energy available for body use while the efficiency of protein deposition may not be altered (Canolty and Koong, 1977). However, besides efficiency of protein deposition there is the additional cost of carcass fat deposition. After meeting energy requirements for body maintenance and the complex processes of protein synthesis and degradation, the surplus ingested energy is then stored as fat. This consequence may not be completely avoidable, even when animals are slaughtered before reaching the age of sexual maturity, because in most mammals fat deposition starts before puberty. The problem of increased degree of fatness in the carcasses of slaughter animals may be avoided to some extent by restricting food energy intake.

When animals were fed *ad libitum*, large differences in feed intake and growth efficiency were observed. The most obvious response found under selection for increased body weight or growth rate is the altered rate of feed intake. Increased feed intake could contribute to significant changes in growth rate even if there are no increases in efficiency. However, as explained previously, in the HL line, increases in growth efficiency boosts the effect of appetite changes at young ages, i.e., it increases feed intake in the selected lines. We still know surprisingly little about this major source of genetic variation in growth rate. Radcliffe and Webster (1976) have suggested, on the basis of their observations, that normal and obese

rats regulate their feed intake to achieve similar rates of protein deposition, despite the fact that they deposit quite different amounts of fat and consume feed at different rates. Their results indicated that the "normal capacity for protein deposition imposed the long term strategy (for appetite control)". While this hypothesis is somewhat vague, it seems to suggest that selection for body weight, in an environment where the rate of feed intake is flexible, presumably searches out animals whose "capacity for protein deposition" is greatest. Results obtained with lines selected for high body weight on restricted levels of feed provide an interesting contrast to those discussed previously. Hetzel (1978) and Yuksel (1979) selected for and achieved gains on restricted levels of feeding. They observed no change in the rate of feed intake when their lines were compared with unselected control mice under *ad libitum* feeding.

A note of caution when interpreting results from laboratory animals: one cannot extrapolate directly to domestic animals, especially ruminants. Also, laboratory animals are usually examined at a specific age, whereas the market demands of the livestock industry are concerned more with the fat content, which in fact is related more directly to weight. Nonetheless, the overriding genetic influence on these variables may have much in common for all species, and laboratory animals are helpful in focusing more clearly on the genetic problems in animal breeding.

V. DIALLEL ANALYSIS OF LITTER TRAITS AT PARTURITION IN TWO ENVIRONMENTS

A. Introduction

Crossbreeding represents an effective means of utilizing available breed resources, combining the advantages of prior selection within breeds (biological types) for economically important traits with the heterosis present in the crossbred progeny and crossbred parents (Dickerson, 1969). In addition to crossbreeding, consideration needs to be given to genotype-environmental interactions. Genotypes react differently to different environments, representing an additional influence and thus are important in animal breeding because genetically similar animals are raised and used under a wide variety of conditions. The problem of evaluating breeding values of animals would be simplified if all effects of genotype and environment on the phenotype were additive (linear effects). Additive effects are part of the heterotic phenomenon but, in addition, non-additive relations (non-linear) between genotype and environment may be the norm as was suggested by Wright (1939). In animal breeding, this means that the effect of an environment on two genotypes is not the same, or put another way, the effect of genotype on the phenotype is not the same in two different environments. Therefore, in the presence of interactions, the phenotypic differences between genotypes A and B is not the same in environments 1 and 2.

The diallel cross method of assessing potential breeding material is a way of using the classical method of genetics, hybridization of

different strains of species, in such a manner as to maximize the information obtainable.

Dickerson (1969, 1973) defined various statistical genetic effects that determine mean performance of breeds and crosses. These include direct and maternal average genetic effects and direct and maternal heterosis which can be estimated from a diallel cross experiment. Gardner and Eberhart (1966) extended the mathematical models of Henderson (1948) and Griffing (1956) by partitioning direct heterosis effects. An expansion of the above models by Eisen *et al.* (1983), included a genetic interpretation and analysis of diallel crosses among random mating lines when maternal effects may be important.

A diallel table may be formed by four methods from the components of the square matrix (Griffing, 1956). The diallel analysis of variance of the data in the diallel table has been reviewed and discussed by several workers (Jinks and Hayman, 1953; Hayman, 1954a, 1954b; Griffing, 1956; Gardner and Eberhart, 1966; and Eisen *et al.*, 1983) with the relationship among, and the analyses for, each method reviewed by Baker (1978) and Eisen *et al.* (1983). The effectiveness of such a mating system lies in the increased breadth of the inferences and confidence in the data, but it also presents a substantial problem in reducing the sheer bulk of the data and effects to comprehensible proportions. Many analyses with meaningful biological interpretations can be made with these data. A single exhaustive analysis is neither practicable nor desirable. As a result of the expansion and generalization of the method of analysis of diallel crosses, it is now possible to obtain statistics from the various measurements of parents and their F_1 progeny generated in diallel crosses. This chapter is

concerned with those analyses relevant to the central topic, elucidation of the genetic basis of variation in body weight among genetically similar mice raised under different environments. Since weight was measured at a number of intervals during growth, an indication of the variation of the parameters with increasing age is provided. This chapter will examine a number of these parameters at parturition. Chapter VI will consider the results during the preweaning, rapid growth phase.

The following analysis of litter size and body weight in a diallel set of crosses among four lines of mice was devised to study the performance of pure lines and crossbred combinations reared in two different environments.

B. Materials and Methods

Design. A 4 x 4 diallel cross was formed with two inbred and two non-inbred lines obtained from the Agriculture Canada Research Station, Lacombe, Alberta. Lines 311 and 312 (inbred base) and 511 and 512 (non-inbred base) and their management were previously described in Chapter II.

The cold environmental room was maintained at 7 $\pm$ 2°C, whereas the control room was maintained at 21 $\pm$ 2°C. The relative humidity was maintained at 45 $\pm$ 5%. Mice were provided with water and feed *ad libitum* (Olde Guilford Breeder Diet[1]) throughout the experiment. Lighting was on a 12-hour photoperiod.

Records taken at parturition included dam weight, litter size and litter weight. Standardization of litter sizes to a common mean was not attempted in order to allow maximum expression of genetic potential

and maternal influences, under the specific environmental conditions. Total mortality was defined as the number born dead and those that died during the first four hours after parturition.

Diallel Table.

A diallel table is a square arrangement of the measures (means and variances) of the progeny of a diallel cross, that is, a set of all possible matings between several genotypes. It consists of n^2 cells, where n = number of genotypes, and comprises n(n-1)/2 entries above and below the diagonal which itself contains n entries.

The progenies constituting the diallel cross are F_1's of all the possible crosses and the four parental strains (Table V.1). The parental strains are represented in the body of the table by the values on the leading diagonal. The matrix is symmetrical.

Least-Squares Equations.

Models for the Analysis of Data from Crossbreeding Experiments

General least-squares procedures for the analysis of data from single crosses only were developed by Henderson (1948). The designs of many crossbreeding or line crossing experiments result in data which may be analyzed in several ways. Three methods of analysis were considered in this section: first, the analysis of type of mating system, either purebred or crossbred plus environment and interactions; second, analysis of sire lines plus dam lines plus environment and interactions; and third, an analysis of all 16 combinations plus environment and interactions. The principal method used in interpretation and discussion of results was the model which had sire and dam as the main effects (Model no. 2). The covariates dam weight and litter size were added to the models for analysis of the trait litter weight at parturition.

Table V.1. A 4 x 4 Diallel Table Designed to Generate Offspring and Maintain Parental (pure) Lines

	Dam Line			
Sire Line	1 (311)	2 (312)	3 (511)	4 (512)
1 (311)	11	12	13	14
2 (312)	21	22	23	24
3 (511)	31	32	33	34
4 (512)	41	42	43	44

The least-squares equations for this model are presented in Table V.2 and the transformation matrix in Table V.3. It can be seen from these equations that while the sums of the coefficients for the heterotic effects equal the coefficient for m (overall mean) in the m equation, none of the sums of coefficients for the other effects equal the coefficient for m. Also, in the sums making up the RHM's (right hand member), only the sum of the RHM's for the heterotic effects equals the sum for the equation. Since the linebreds are not used in estimating the general combining abilities or maternal abilities, and are not involved in estimating specific or sex-linked effects, several cells in the table contain no entries. Again, it is noted that in the segment of the coefficient matrix corresponding by row and column to the general combining ability effects, there are entries in the off-diagonal elements while in the segments corresponding to the other effects, only zeros appear in the off-diagonals.

Model #1

y = m + mating system + environment + interactions + error

where m = overall mean

mating system = 1 (purebred) or 2 (crossbred)

environment = 1 (control) or 2 (cold)

plus all 2-factor interactions and error source of variation.

Model #2

y = m + sire + dam + (SxD) + environment + (SxE) + (DxE) + error

where m = overall mean

sire = 1, 2, 3, 4 lines

dam = 1, 2, 3, 4 lines

environment = 1 (control) or 2 (cold)

plus all 2-factor interactions and error source of variation

Table V.2. Least squares equations for 4 x 4 diallel analysis.

	μ	$\hat{a}_h$	p_{111}	g_{21}	m_{2j}	c_{21j}	r_{21j}	RHM
μ	$n_{...}$	$n_{h..}$	n_{111}	$n_{21.}+n_{2.1}$	$n_{2.j}$	$n_{21j}+n_{2j1}$	n_{21j}	$Y_{...}$
a_h	$n_{h..}$	$c^{n_{j..}}$	n_{111}	$n_{21.}+n_{2.1}$	$n_{2.j}$	$n_{21j}+n_{2j1}$	n_{21j}	$Y_{h..}$
p_{111}	$n_{1..}$	$n_{1..}$	$o^{n_{1..}}$	-	-	-	-	$Y_{h..}$
g_{q1}	$n_{21.}+n_{2.1}$	$n_{21.}+n_{2.1}$	-	$n_{21j}+n_{2j1}$ $n_{21.}+n_{2.1}$ $n_{21j}+n_{2j1}$	$n_{2.j}$	$n_{21j}+n_{2j1}$	n_{21j}	$Y_{21.}+Y_{2.1}$
m_{2j}	$n_{2.j}$	$n_{2.j}$	-	$n_{2.j}$	$o^{n_{2.j}}$	n_{21j}	n_{21j}	$Y_{2.j}$
c_{2kj}	$n_{21j}+n_{2j1}$	$n_{21j}+n_{2j1}$	-	$n_{21j}+n_{2j1}$	n_{21j}	$o^{n_{21j}+n_{2j1}}$	n_{21j}	$Y_{21j}Y_{2j1}$
r_{21j}	n_{21j}	n_{21j}	-	n_{21j}	n_{21j}	n_{21j}	$o^{n_{21j}}$	Y_{21j}

Adapted from Harvey (1979).

Table V.3. Coefficients for the orthogonal comparisons: $y = \mu + a_h + p_{ii} + g_{2i} + g_{2j} + M_{2j} + c_{2ij} + r_{2ij} + e_{jijk}$.
Purebred effects estimated independently of general combining ability and maternal effects (adopted from Harvey, 1975).

Estimated effects	Sire/dam combinations (including reciprocals)															
	S_{11}	S_{12}	S_{13}	S_{14}	S_{21}	S_{22}	S_{23}	S_{24}	S_{31}	S_{32}	S_{33}	S_{34}	S_{41}	S_{42}	S_{43}	S_{44}
μ:	3	1	1	1	1	3	1	1	1	1	3	1	1	1	1	3
a_1:	3	-1	-1	-1	-1	3	-1	-1	-1	-1	3	-1	-1	-1	-1	3
p_{111}:	18	0	0	0	-6	0	0	0	0	0	-6	0	0	0	0	-6
p_{122}:	-6	0	0	0	0	18	0	0	0	0	-6	0	0	0	0	-6
p_{133}:	-6	0	0	0	0	-6	0	0	0	0	18	0	0	0	0	-6
g_{21}:	0	6	6	6	0	0	-3	-3	0	-3	0	-3	0	-3	-3	0
g_{22}:	0	0	-3	-3	6	0	6	6	-3	0	0	-3	-3	0	-3	0
g_{23}:	0	-3	0	-3	-3	0	0	-3	6	6	0	6	-3	-3	0	0
m_{21}: $\frac{1}{24}$	0	-6	-6	-6	6	0	0	0	6	0	0	0	6	0	0	0
m_{22}:	0	6	0	0	-6	0	-6	-6	0	6	0	0	0	6	0	0
m_{23}:	0	0	6	0	0	0	6	0	-6	6	0	-6	0	0	6	0
c_{212}:	0	4	-2	4	0	-2	-2	-2	-2	0	4	4	-2	-2	4	0
c_{213}:	0	-2	4	-2	-2	0	-2	4	4	-2	0	-2	-2	4	-2	0
r_{212}:	0	6	-3	-3	-6	0	3	3	3	-3	0	0	3	-3	0	0
r_{213}:	0	-3	6	-3	3	0	-3	0	-6	3	0	3	3	0	-3	0
r_{223}:	0	3	-3	0	-3	0	6	-3	3	6	0	3	0	3	-3	0

Model #3

y = u + individual cell + environment + 2-way interactions + error

where u = overall mean

individual cell = 1, 2, ... the genetic sets of offspring

environment = 1 (control) or 2 (cold)

plus all 2-factor interactions plus error source of variation.

Statistical Analysis

The principal method used in interpretation and discussion of the results was the model which had sire and dam as the main effects (i.e., Model #2). The use of the other methods was considered when it added further to the interpretation of the results.

The mathematical models used in the analyses were formulated by Henderson (1948), and extended by Kidwell *et al.* (1960) and Harvey (1975).

Litter size and number born alive (considered measures of fertility) were assumed to be traits of sire and dam lines. Litter size at birth, number born alive and litter weights were analysed by least-squares procedures (Harvey, 1975) based on the model.

The mathematical model for the underlying analysis is:

$$Y_{hijk} = u + a_h + p_{ii} + g_i + g_j + m_j + c_{ij} + r_{ij} + e_{hijk}$$

(Harvey, 1975)

where Y_{hijk} = the k^{th} observation on the progeny of a mating of a dam from the j^{th} line with a sire of the i^{th} line in the h^{th} type of breeding (purebred or crossbred);

u is the overall mean;

a_h = an effect common to all progeny of the h^{th} type of breeding (linebred or crossbred), the difference between these effects being an estimate of heterosis;

p_{ii} = an effect common to all progeny of a mating between a dam of the i^{th} line and a sire of the i^{th} line;

g_i (g_j) is the general combining ability effect for the ith (j^{th}) line;

m_j is the maternal effect for the jth line of dam;

c_{ij} is the specific combining ability effect;

r_{ij} is the reciprocal effect; and

e_{hijk} is the random error.

The g_i (g_j) are assumed to be one-half the additive genetic value (breeding value) of the ith (jth) line, and the value is expressed as a deviation from *m*. The m_j measure the pre-natal and post-natal mothering ability of a line, and each is a function of the genotype of a line rather than of the genes transmitted to the female progeny of the line. The c_{ij} are effects in addition to the g_i and m_j effects, and are measured over the progeny of the ith line of sire with the jth line of dam and the progeny of the jth line of sire with the ith line of dam. The c_{ij} measure how much better or poorer than average are the means of reciprocal matings than would be expected on the basis of exact knowlege of the additive genetic values and maternal values of the lines. The r_{ij} are effects in addition to the additive genetic, maternal, and specific effects and are measures of the differences between reciprocal crosses after account has been taken of the differences in maternal ability between the ith line and the jth line. For a more detailed discussion of these effects, refer to Henderson's thesis (1948).

The degrees of freedom for the model described are calculated as shown below (for crossbreds):

Source of Variation	Degrees of Freedom
Total	n.. -1
General combining ability	p-1
Maternal ability	p-1
Specific combining ability	[p(p-3)/2]
Residual reciprocal effects	[p(p-3)/2] + 1
Error	n..-p(p-1)

C. Results

All main effects (sire, dam, environment) and 2-factor interactions were significant ($P < .05-.01$) for percent mortality (Table V.4). Litter weight was significantly influenced by all effects except dam, dam x environmental and covariate 1 (dam weight).

Genetic comparisons were of interest for determining if specific crossbred combinations were different from the four parental lines for any of the traits measured. Although the mean squares interactions were not significant for any of the traits analyzed under the sire x dam x sex subclass model, main effects (sires, dams, and environment) for percent mortality and litter weight were significant ($P < 0.05$). Deaths did not appear to involve any specific pathology and were equally distributed between the sexes. Dams in the cold appeared alert and active prior to parturition, but thereafter during the preweaning period, they were often hunched and showed piloerection. Health was generally good; however, some mice had inflamed ears, the margins of which sometimes became necrosed, and some tails were sloughed. Mice

raised in the cold room had an overall percent mortality of 63% compared to the 7.6% for mice in the control room. Average birth weight was higher ($P < 0.1$) for mice born into the control room, 1.64 g compared to 0.73 g for mice born into the cold room. However, the environment had the greatest influence on mortality (survival).

Mating System. Mating system was significant ($P < .05$) for litter weight and percent mortality. The cold environment significantly influenced the performance of the purebreds vs crossbreds for the above two traits. Average litter weight for the crossbreds was 1.7 g heavier than the purebreds. Percent mortality was 13.25% lower for the crossbreds than for the purebreds.

Sire Line. Line of sire was significant for dam weight at parturition ($P < .01$) and litter weight ($P < .05$). Mean squares and least-squares means for parturition weight (Table V.4 and V.5) show that the two highly selected lines (312 and 512) were heaviest at birth. Since the sire contributed only genetically to the performance of the progeny, any comparisons must include this consideration. No significant sire line effects existed for total number of pups born; percent mortality and average birth weight. These results suggest that the sire contribution to these traits was of little consequence.

Dam Line and Maternal Influence. Line of dam influence was non-significant for all birth traits; litter size, litter weight, and percent mortality (Table V.5). Line 512 consistently had the poorest mothering ability, except in survival rate (% mortality) which was the highest. Line 511 showed the best mothering ability for total number of pups born and total litter weight at birth and placed second in survival rate and average birth weight of pups. Line 312 had the

Table V.4. Analyses of variance of biological traits at parturition in two environments[a].

Source	df	Mean squares	
		Litter wt.	% mortality
Sires (S)	3	10.28	2494.03†
Dams (D)	3	2.67	324.21
Environment (E)	1	111.77**	107388.99**
S x D	9	8.69†	1296.21
S x E	3	8.57	177.46
D x E	3	4.98	1065.49
Covariate 1[b]	1	35.20	4430.44*
Covariate 2[c]	1	1399.25**	1262.4[illegible]
Error	119	6.33	1057.30

[a]Environment #1 = 21 ± 2°C; Environment #2 = 7 ± 2°C.

[b]Adjusted by covariance analysis for linear effects of dam weight at parturition.

[c]Adjusted by covariance analysis for linear effects of litter size at parturition.

**P < .01.

*P < .05.

†P < .10.

Table V.5. Least-squares means of birth traits in two environments (E1, E2)[a].

	Dam wt. (g)[b]		Litter size[c]		Litter wt. (g)[b]		% mortality[b]	
	E1	E2	E1	E2	E1	E2	E1	E2
Cell Code Number								
11	30.9	31.6	8.9	9.1	14.0	10.4	2.3	54.1
22	39.8	36.7	7.7	7.8	14.8	13.4	0.0	83.3
33	37.3	36.2	8.0	7.6	13.9	8.8	20.0	93.3
44	37.9	38.9	7.4	7.4	15.3	9.0	24.4	83.5
Cross[d]								
12	31.9	29.2	9.6	9.1	15.1	11.6	0.5	60.2
13	37.2	32.4	8.1	7.6	15.0	12.3	0.7	61.1
14	30.9	30.0	10.0	9.3	13.5	12.2	4.3	59.5
21	35.2	35.4	8.9	11.3	14.1	12.4	1.4	70.1
23	34.8	36.0	10.1	7.9	14.4	12.1	5.6	50.0
24	34.8	34.7	10.1	9.0	14.8	15.4	7.3	13.6
31	33.0	31.0	8.7	7.5	14.3	10.8	5.9	54.7
32	33.3	36.4	9.3	7.7	11.3	13.4	5.3	79.3
34	36.9	35.9	7.8	7.4	14.9	12.5	5.9	52.2
41	46.0	35.6	6.7	10.4	13.9	14.1	4.6	70.3
42	40.0	42.1	7.1	7.2	15.2	10.7	1.0	60.2
43	37.7	38.5	10.2	6.8	15.8	11.5	9.7	71.1
μ[e]	36.1	35.1	8.7	8.3	14.4	11.9	7.5	63.5
SE[f]	2.2-3.7	1.9-3.1	1.2-2.1	1.1-1.8	6-1.1	1.1-1.8		

[a] Environment #1 = 21 ± 2°C; #2 = 7 ± 2°C.

[b] Adjusted by covariance analysis for litter size at parturition, within each environment.

[c] Adjusted by covariance analysis for dam weight at parturition, within each environment.

[d] Crossbred progeny (12) generated by 4 x 4 diallel mating system.

[e] Overall least square means.

[f] Range of subclass standard errors.

highest average birth weight of pups but this may be due to it having the highest percent mortality. Line 311 exhibited below average mortality (%) in both environments and the lowest dam parturition weight.

Environmental Influence. The environment was the most influential factor of all the effects studied (Table V.4). It was a significant factor ($P < .01$) in lowering the litter weight at birth for mice born into the cold environment. Also, as mentioned previously, it was a highly significant determinant of percent mortality.

Least-squares means are given in Table V.5 for dam traits in the two environments. In each category the mice in the control room performed significantly better than those born in the cold room.

Heterosis. Table V.6 is a presentation of the least-squares means for the dam traits analyzed by mating system (Purebred vs. Crossbred) and environmental temperature (Control vs. Cold). Although not significant, crossbred litter sizes were larger and weighed heavier than offspring born from purebred matings, in both environments (Table V.6). Percent mortality was significantly greater for pureline litters, in both environments.

General Combining Ability (GCA). Ranking of the lines for GCA of dam body weights at parturition was 512 > 312 > 511 > 311, reflecting primarily the weight divergence of the lines which resulted from their history of selection for high six-week body weight. Line ranking for GCA of total born and litter weight was: 312 > 512 > 311 > 511. However, this pattern was not followed for line differences in percent mortality: 511 > 512 > 311 > 312. General combining ability was not significant at parturition for litter weight.

Table V.6. Least-squares means for differences between purebred and crossbred litters born into different environments[a].

	Litter size		Litter wt. (g)		% mortality	
	E1	E2	E1	E2	E1	E2
Overall mean[b]	8.49	8.07	14.2	11.4	9.3	69.2
Purebreds	7.99	7.99	13.6	10.4	12.8	78.7
Crossbreds	8.98	8.15	14.8	12.4	5.8	59.8

[a]Environment #1 = 21 ± 2°C; Environment #2 = 7 ± 2°C.

[b]Adjusted by covariance analysis for dam weight at parturition.

Litter Size. The effect of litter size on litter birth weight was highly significant ($P < .01$) for mice born into both environments. Adjusting litter size at birth by covariance analysis on a within environment basis permitted line comparisons for the various traits, assuming equal litter sizes. Least-squares analysis for several birth traits are presented in Table V.7. Litter weight was significantly heavier for mice born into the control room although litter size was not significantly different. Environment influence was the most consistent factor in affecting total litter weight ($P < .01$), average litter weight ($P < .01$) and percent mortality ($P < .01$).

Covariate Analysis. The significance of including litter size and/or dam weight in the model as covariates is presented in Tables V.8 and V.9. In the control room, litter size (covariate) was shown to affect litter weight and percent mortality. Percent mortality was also influenced by litter size in the control room. The results for the cold room were different, e.g. litter size was most influential ($P < .01$) in affecting litter weight, whereas dam weight significantly affected ($P < .05$) percent mortality. Adjusted total litter weight at parturition is presented in Table V.10. Dam line 512 gave birth to the heaviest litters in mating with sire lines 312 and 512.

D. Discussion

In many experiments with a variety of organisms and traits, inbreds have often been found to be more susceptible to environmental variation than crossbreds. Lerner (1954), Waddington (1957), Kidwell and Howard (1969) and Barrett and Neil (1972) have all discussed this phenomenon and given various theories to account for its occurrence, but the

Table V.7. Least-squares analyses of variance showing mean squares and probability for main effects and 2-factor interactions for five traits at parturition.

Source	df	Dam wt. (g)		Total born[a]		Litter wt. (g)		% mortality		Avg. litter wt. (g)	
		Mean sq.	Prob.	Mean sq.	Prob.	Mean sq.	Prob.	Mean sq.	Prob.	Mean sq.	Prob.
Sire (S)	3	479.75	.01	16.38	.19	57.43	.05	1523.23	.24	.038	.68
Dam (D)	3	19.82	.62	1.53	.93	0.66	.99	195.73	.90	.096	.28
Envt. (E)	1	22.53	.41	3.77	.54	177.76	.01	110235.24	.01	.223	.08
S x D	9	36.36	.37	4.60	.90	20.73	.47	1291.75	.30	.038	.87
S x E	3	2.71	.97	0.66	.98	14.90	.56	208.86	.90	.018	.87
D x E	3	6.85	.89	14.74	.23	42.73	.12	1062.75	.40	.089	.31
Error	121	33.21	--	10.19	--	21.58	--	1077.54	--	.074	--

[a]Includes pups stillborn.

Table V.8. Analyses of variance of biological traits at parturition in the control environment.

Source	df	Mean squares	
		Litter wt.	% mortality
Sires	3	2.03	815.56†
Dams	3	2.64	203.91
Covariate 1[a]	1	13.27	2.87
Covariate 2[b]	1	839.15**	1339.02*
Error	58	2.36	312.82

[a]Covariate 1 - Adjusted by covariance analysis for linear effects of dam weight at parturition.

[b]Covariate 2 - Adjusted by covariance analysis for linear effects of litter size at parturition.

**P < .01.

*P < .05.

†P < .10.

Table V.9. Analyses of variance of biological traits at parturition in the cold environment.

Source	df	Mean squares	
		Litter wt.	% mortality
Sires	3	17.04	2076.48
Dams	3	5.06	1874.61
Covariate 1[a]	1	18.64	7274.43*
Covariate 2[b]	1	661.67**	4947.13
Error	68	9.96	1657.44

[a]Covariate 1 - Adjusted by covariance analysis for linear effects of dam weight at parturition.

[b]Covariate 2 - Adjusted by covariance analysis for linear effects of litter size at parturition.

**$P < .01$.

*$P < .05$.

Table V.10. Least-squares means for litter weight at parturition for sire by dam subclasses, line of sire and line of dam (combined environments).

Sire/Dam	311	312	511	512	$\bar{y}^*_{1.}$	$\bar{y}_{1.}$
			Average litter weight (g)[e]			
311	<u>12.0</u>	13.2	13.7	12.8	13.2	12.9
312	13.1	<u>14.0</u>	13.3	14.9	13.8	13.6
511	12.5	13.1	<u>11.2</u>	13.7	13.1	12.6
512	13.5	12.6	13.9	<u>12.1</u>	13.3	13.0
$\bar{y}^*_{.1}$	13.0	13.0	13.6	13.8	13.4[b]	-
$\bar{y}_{.1}$	12.8	13.2	13.0	13.4	12.3[c]	-
			Total litter weight (g)[e]			
311	<u>82.48</u>	78.02	93.71	83.67	85.13	83.97
312	91.62	<u>83.20</u>	91.52	106.08	96.41	93.11
511	98.86	93.27	<u>81.10</u>	94.38	95.50	91.90
512	89.50	88.43	98.27	<u>103.92</u>	92.07	95.03
$\bar{y}^*_{.1}$	93.33	86.57	94.50	94.71	92.28[b]	5.44-8.99[d]
$\bar{y}_{.1}$	90.12	85.73	91.15	97.01	87.18[c]	

[a]The terms $\bar{y}_{1.}$ ($\bar{y}_{.1}$) represent the sire (dam) marginal means including the parental lines; $\bar{y}^*_{1.}$ ($\bar{y}^*_{.1}$) are the corresponding means excluding the parental line; parental means are underlined.

[b]Crossbred mean ($\bar{y}_c$).

[c]Parental line mean ($\bar{y}_a$).

[d]Range of subclass standard errors with 16 to 51 observations/subclass.

[e]Adjusted by covariance analysis for linear effects of litter size.

biological basis has not yet been fully determined. Maternal influences refer to those conditions which influence the expression of the maternal effects. These effects are the measured phenotypic expressions from influences of the mother on a trait measured in her offspring, apart from the direct influence of the genes she transmits, and represent both her genotype and phenotype. From the standpoint of the offspring, maternal influences may be considered as environmental in nature, conditioning the expression of the offspring's genotype for the trait measured.

For many species significant sire and dam breed effects on birth weight have been reported (in sheep, Jamison *et al.* 1961; Fahmy *et al.* 1972; in beef cattle Cundiff, 1970; and in mice El Oksh *et al.* 1967). Differences among dam breeds were not significant (Table V.7) thus suggesting that the maternal environment was not an important factor affecting the preweaning performance of pups in these breeds. Reports to the contrary exist (Eisen *et al.* 1983; Horstgen-Schwark *et al.* 1984), but these authors did not have the additional complication due to environment. The present results are also contrary to those reported by Falconer (1947); Bateman (1954); Cox *et al.* (1959); Legates (1972); Rutledge *et al.* (1972); Brandsch and Kadny (1977); Hayes and Eisen (1979). Perhaps the large environmental influence on the maternal effects within the present study masked their expression, resulting in the major difficulty of attempting to separate the transmitted and direct effects of the dam on the traits measured at parturition.

Heterosis may be defined as the occurrence of greater fitness in crossbred (outbred) than in purebred (inbred) individuals of the same species. An index of fitness could include such parameters as the

number born and mortality rates. Interpreting the results of purebred vs. crossbred offspring in the two environments would give a clearer indication of the significance for 'heterosis' under a cold stress. An interesting question is how crossbreeding influences the performance under extreme adverse environmental influences such as cold temperature. The well established effect of heterosis on reproductive performance seems to be enhanced in a cold environment. For example, Barnett and Coleman (1960) and Barnett (1973) adopted results similar to the present study in the context that their F_1 populations differed from the purebred strains in two major features: (1) large litter sizes at birth and (2) higher mortality of young born into a cold environment. Most deaths took place during the first ten days of life. Often deaths involved losses of the entire litter.

Under the cold temperature, the superior performance of the crossbreds relative to their purebred contemporaries was interpreted as a clear indication of the 'heteroic effect' on female reproduction traits. This was most evident for the fitness traits of total born and percent mortality. Inbreeding depression (discussed in Chapter 3) may have contributed to the poorer performance of purebred mice in both environments. However, two additional factors may be considered an explanation for the performance of the crossbred progeny. The first is energy conservation. Heat loss was reduced by piloerection and by posture, and probably by peripheral vasoconstriction as well. The mice were possibly also more efficient heat producers if they developed brown fat in the cold (Jansky, 1973; Heldmaier, 1974) and with it a capacity for non-shivering thermogenesis. The second factor is *ad libitum* feeding. Although not measured quantitatively, feed intake

was markedly greater in the cold and in the long term was tailored to energy demand. Feed provides energy for physical activity and growth in addition to resting metabolic requirements and, as reported by Bateman and Slee (1979), mice exposed to cold temperatures had higher maintenance requirements and higher feed consumption than mice raised at normal room temperatures (approx. 21°C).

Both of the above factors complement the effect of hybridity in the cold environment. The superior vigour, in the sense of resistance to cold of the young F_1 mice is evident by their ability to respond adaptively to the cold stress. This may be interpreted as an increase in resourcefulness of the genotype: natural selection favoring the more versatile individuals (heterozygotes) which are better able to buffer (respond to) the unfavorable environment.

These observations are in agreement with the hypothesis that heterozygosis confers a greater degree of homeostasis in respect of disturbances in the environment - an example of heterosis or hybrid vigour.

General combining ability as defined by Sprague and Tatum (1942) is as follows: 'to designate the mean performance of a line when expressed as a deviation from the mean of each line in all its crosses'. It is the average value of all F_1's having this line as one parent, the value being expressed as a deviation from the overall mean of crosses. Line 512 exceeded all other lines for general combining ability but, as remarked earlier, this line had several particular advantages including source (from the non-inbred foundation 5), large population size (hence a slower rate of inbreeding), and a history of selection for large body size.

Highly significant maternal effects were shown by Carmon (1963) in a diallel cross of four inbred lines for weights at 21 and 45 days. Significant maternal effects were also reported by Kidwell and Howard (1969) which accounted for an increasing proportion of the total variance for weights from the first through the fourth week. Thereafter, the maternal influence steadily declined until no appreciable effect remained after ten weeks. Thus, when general combining ability effects are not significant, it does not necessarily mean that they do not exist. Generally, low values indicate a rather low proportion of additive genetic variance.

As defined by Sprague and Tatum (1942): 'specific combining ability (SCA) is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved.' In these experiments SCA was not consistent between the two environments, indicating the significant influence due to environmental temperature.

Physiologically, cold stress may decrease litter weight, but not significantly affect ovulation rate, conception or embryonic survival. Barnett and Manly (1956) found that average litter size was reduced in the cold environment (-3°C) as compared to the temperate environment. However, their findings were based on females from an inbred strain ($C_{57}BL$) and if we examine the four parental lines, the average litter size is less than the overall mean.

The adjusted litter weights at parturition for the 16 genetic combinations were compared across both environments. Crossbred litters tended to be slightly heavier at birth, but with several exceptions the dam line 512 had the heaviest litters and the combination with 312

(sire) and 512 (sire) was indeed the heaviest. Thus the F_1 of the two lines selected for weight gave the best weights at parturition.

The more pups there are in a litter, the smaller each is at birth and the slower they grow. In comparing our growth data at diffrent environmental temperatures we must take this effect into account, since early mortality substantially reduced the average litter sizes of litters reared in the cold environment as compared with those reared in the temperate environment. One method of accounting for unequal litter sizes is to have litter size as a covariate in the linear model. In this experiment litter size had a highly significant effect on litter weight ($P < .01$) and therefore including it in the model reduced the error term (error mean square) by accounting for more of the unexplained variation.

Perhaps one reason for the similar litter size at birth between the two environments (Table V.5) was the fact that the dams were all on *ad libitum* feeding. Since feed intake measurements were not taken it is impossible to determine the amount of feed eaten. However, observations made at each feeding indicated an appreciable difference in the amount of feed eaten by dams in the cold environment (more feed than under control conditions). Thus due to the additional energy consumed may have allowed the body to function quite normally even in a stressful environment.

Clearly, the outbred lines (511 and 512) performed much better than inbred lines (311 and 312) when used in crossbred combinations (Table V.10). However, the two best combinations for total litter weight (adjusted) were 312 x 512 and 512 x 512 - both highly selected lines and from large population sizes. This would indicate that both selection pressure and population size were influential in determining

the total litter weight obtained. Would a similar trend be obtained in our pig breeding operations? Also, the percent mortality recorded is a function of litter size, and this too may have implications to pig husbandry. Standardization of litter size to a number that will maximize profits is routinely done today by pig operation managers. Up to a point, increasing the number of offspring will increase the total litter weight, but shortly a level of production is reached in which there is a negative return for each additional offspring added to the litter. This point is illustrated by the comparison of unadjusted vs. adjusted litter weights (Table V.10).

VI. DIALLEL ANALYSIS OF LITTER GROWTH TRAITS IN TWO ENVIRONMENTS

A. Introduction

Present emphasis on crossbreeding in livestock operations has dealt almost exclusively with considering advantages of breed crosses, with little attention given to selection history of breeds and to the environmental conditions under which they will be raised (Wilham, 1970; Johnson, 1981). Understanding how previous selection for a trait(s) influences crossbred performance for an array of traits under a variety of environmental conditions has received scant attention in livestock breeding programs.

Selection in mice has led to the development of lines that differ markedly in growth rate and growth efficiency (Bailey *et al.* 1984). The objective of the present study was to utilize these lines as models in a 4 x 4 diallel cross to evaluate genetic effects of pureline and crossline progeny, each raised in two environments. The diallel analysis of Kidwell et al. (1960), Gardner and Eberhart (1966) and extended by Harvey (1975), was used to provide a framework for genetic interpretation of the results.

The traits litter size and litter weight at weaning, chosen as measures of productivity, have relevance to production in farm animals, particularly pigs, being traits which contribute substantially to economic return.

B. Materials and Methods

Genetic Analyses

Diallel table

The four lines used in the 4 x 4 diallel cross were described in Chapters 2 and 5.

Statistical Analysis of Preweaning Growth Traits

Maternal effects (M_j) measure the prenatal and postnatal mothering ability of the line and are a function of the genotype of the line. They take into account the dams milk producing ability plus any maternal ability associated with behaviour.

General combining ability (g_{ij}) is the average performance of a line in crosses (Sprague and Tatum, 1942) for direct genetic effects only.

Specific combining ability c_{ij} can be used as a measure of performance for a specific cross (Sprague and Tatum, 1942; Henderson, 1948).

The model employed in this analysis was similar to that given in Chapter V (page 58) with the exception that sex effects are now included.

Dam weight and litter size were two covariates included in the model. Dam weight was included in order to determine if progeny performance during the preweaning period was influenced by dam weight. Litter size was used as a covariate to establish whether the number of pups in the litter influenced the average weaning weight.

C. Results

Environmental Effects. Large environmental effects ($P < 0.001$) were present for the growth traits evaluated. The main effects from

the analyses are presented in Tables VI.1 and VI.2. Weaning weight and tail length were significantly affected by the environment in all analyses.

Dam Line. Line rankings for dam weights were 512 > 312 > 511 > 311 ($P < .001$) while ranking for 21-day weight and tail length measurements of the progeny were 512 > 511 > 311 > 312 ($P < .001$). Although there is close agreement between tail length and body weight, this doesn't account for the differences in ranking due to dam vs sire line. The selected, non-inbred line 512, showed consistent response in each variable whereas the selected, inbred line 312 showed inconsistency.

Sex Effects. Sex differences were significant ($P < .01$) for most traits but differences were small (e.g., males > females by 7% at weaning) and the contribution of sex to the total variance was not highly significant ($P < 0.12$).

Table VI.1. Least squares means for mating systems,[1] sex[2] and environment[3]: main effects plus interactions for 21-day individual weight and tail length.

	No. obs.	21-day indiv. wt. (g)	21-day indiv. tail length (cm)
Overall mean	763	12.18 ± 0.15	5.85 ± 0.03
Purebreds	195	11.76 ± 0.26	5.78 ± 0.06
Crossbreds	568	12.60 ± 0.13	5.91 ± 0.03
Sex			
Males	393	12.47 ± 0.19	5.88 ± 0.04
Females	370	11.89 ± 0.20	5.81 ± 0.04
Environment			
Control	547	13.79 ± 0.14	7.10 ± 0.03
Cold	216	10.57 ± 0.26	4.60 ± 0.05
[1]Mat. Sys. x Sex 1	88	11.83 ± 0.34	5.78 ± 0.07
[1]Mat. Sys. x Sex 2	107	11.69 ± 0.34	5.79 ± 0.07
[2]Mat. Sys. x Sex 1	305	13.11 ± 0.17	5.99 ± 0.04
[2]Mat. Sys. x Sex 2	263	12.08 ± 0.20	5.84 ± 0.04
[1]Mat. Sys. x Environ. 1	156	13.70 ± 0.23	7.15 ± 0.05
[1]Mat. Sys. x Environ. 2	39	9.83 ± 0.47	4.41 ± 0.10
[2]Mat. Sys. x Environ. 1	391	13.88 ± 0.14	7.05 ± 0.03
[2]Mat. Sys. x Environ. 2	177	11.31 ± 0.22	4.78 ± 0.05
Sex 1 x Environ. 1	270	14.12 ± 0.20	7.14 ± 0.04
Sex 1 x Environ. 2	123	10.83 ± 0.32	4.63 ± 0.07
Sex 2 x Environ. 1	277	13.45 ± 0.18	7.06 ± 0.04
Sex 2 x Environ. 2	93	10.32 ± 0.35	4.56 ± 0.08

[1]Mating system refers to: 1 = purebred; 2 = crossbred.

[2]Sex: 1 = males; 2 = females.

[3]Environment: 1 = control; 2 = cold.

Table VI.2. Least squares means for the main effects of sire line, dam line, sex[1] and environment[2] growth traits at weaning.

Source		21-day indiv. wt. (g)	21-day indiv. tail length (cm)
Overall mean		12.5 ± 0.12	5.9 ± 0.02
Sire line:	311	11.5 ± 0.25	5.7 ± 0.05
Sire line:	312	12.9 ± 0.25	5.7 ± 0.04
Sire line:	511	12.7 ± 0.23	6.1 ± 0.04
Sire line:	512	13.0 ± 0.20	6.2 ± 0.04
Dam line:	311	12.4 ± 0.24	5.9 ± 0.05
Dam line:	312	11.6 ± 0.21	5.6 ± 0.04
Dam line:	511	12.7 ± 0.22	6.0 ± 0.04
Dam line:	512	13.3 ± 0.24	6.1 ± 0.05
Sex:	1	12.8 ± 0.15	5.9 ± 0.03
Sex:	2	12.1 ± 0.17	5.8 ± 0.03
Environment:	1	14.0 ± 0.12	7.1 ± 0.02
Environment:	2	11.0 ± 0.20	4.7 ± 0.04

[1]Sex code: 1 = males; 2 = females.

[2]Environment: 1 = control; 2 = cold.

Heterosis. Heterotic effects, defined as the difference between the least-squares means of all crossbreds and the least-squares means for all purebreds was significant (Tables VI.3 to VI.4) for all main effects for 21-day individual weights. Two-factor interactions were significant for subclasses mating system x sex ($P < 0.07$) and mating system x environment ($P < 0.05$) for the trait 21-day individual weights.

Sire/Dam Subclasses. Line ranking for 21-day weight (weaning) were highly significant ($P < .01$) with a line ranking of 512 > 312 > 511 > 311 in the control room compared with the ranking of 312 > 512 > 511 > 311 in the cold room. Maternal effects for dam weights were highest for line 512 in both environments, indicating that over time (selection plateaued prior to 1979) these lines had responded to selection pressure for increased body weights. However, for the traits offspring body weight and tail length of the mice in the cold room, the unselected line 311 was the highest. Comparing the least-squares means (Tables VI.5 to VI.7) for 21 day body weights for this line in both environments, one finds that their performance was lower than the overall mean within each environment.

General Combining Ability and Maternal Effects. The general combining ability for progeny weights at weaning in each environment was highest for line 512 (Table VI.8). Altogether, differences due to g_{ij} were small between the 511, 311 and 312 lines. Ranking of the lines for m_j were almost identical for both environments: 512 > 312 > 511 > 311.

Table VI.3. Least square means for interactions: sire x environment and dam by environment subcasses[a]: growth traits at weaning.

Source		21-day indiv. body wt. (g)	21-day tail indiv. length (cm)
Sire:	Environment[a]		
311	1	13.7 ± 0.25	7.1 ± 0.05
311	2	9.2 ± 0.43	4.2 ± 0.09
312	1	14.3 ± 0.29	6.9 ± 0.06
312	2	14.0 ± 0.40	4.5 ± 0.08
511	1	13.4 ± 0.20	7.1 ± 0.04
511	2	12.0 ± 0.41	5.0 ± 0.80
512	1	14.7 ± 0.23	7.2 ± 0.05
512	2	11.3 ± 0.33	5.0 ± 0.07
Dam:	Environment[a]		
311	1	14.0 ± 0.28	7.1 ± 0.06
311	2	10.9 ± 0.39	4.7 ± 0.08
312	1	12.9 ± 0.21	6.7 ± 0.04
312	2	10.3 ± 0.38	4.4 ± 0.08
511	1	14.4 ± 0.26	7.3 ± 0.05
511	2	10.9 ± 0.35	4.7 ± 0.07
512	1	14.8 ± 0.22	7.3 ± 0.04
512	2	11.9 ± 0.44	5.0 ± 0.09

[a]Environment: 1 = control room, 21°C; 2 = cold room, 7°C.

Table VI.4. Analyses of variance of biological traits for mating systems[a] in two environments.

Environment	Source	df	Mean squares	
			Litter wt.	% mortality
Control	Mating system	1	.05	389.11
	Covariate 1[b]	1	17.68	155.60
	Covariate 2[c]	1	888.34**	1564.57*
	Error	63	2.38	335.09
Cold	Mating system	1	51.57*	6120.4*
	Covariate 1[b]	1	14.60	2544.9
	Covariate 2[c]	1	790.23**	2662.0
	Error	74	9.59	1621.2

[a]Mating systems are purebreds vs crossbreds.

[b]Adjusted by covariance analysis for dam weight at parturition.

[c]Adjusted by covariance analysis for litter size at parturition.

**$P < .01$.

*$P < .10$.

Table VI.5. Least-squares means for sire by dam subclasses, line of sire and line of dam[a]: control room.

Sire	Dam 311	312	511	512	$\bar{y}_{i.}$*	$\bar{y}_{i.}$
			21-day progeny body wt. (g)			
311	13.4	12.4	14.5	13.9	13.6	13.6
312	14.9	12.8	13.9	15.5	14.8	14.3
511	14.3	13.2	12.7	13.2	13.6	13.3
512	13.6	13.2	15.9	16.2	14.2	14.7
$\bar{y}_{.i}$*	14.3	12.9	14.8	14.2	14.0[b]	0.4-0.7[d]
$\bar{y}_{.i}$	14.1	12.9	14.2	14.7	13.8[c]	
			Adj. 21-day progeny body wt. (g)[e]			
311	12.8	13.5	15.9	15.6	15.0	14.4
312	14.6	13.4	13.9	15.4	14.6	14.3
511	14.7	14.1	11.4	14.8	14.5	13.7
512	14.0	13.8	16.0	16.5	14.6	15.1
$\bar{y}_{.i}$*	14.4	13.8	15.3	15.3	14.7[b]	0.9-1.8[d]
$\bar{y}_{.i}$	14.0	3.7	14.3	15.6	13.5[c]	
			Adj. total weaning wt. (g)[e]			
311	103.5	102.2	114.1	118.0	111.4	109.4
312	117.2	107.5	113.3	124.1	118.2	115.5
511	117.2	113.0	98.8	113.8	114.7	110.7
512	111.8	111.1	125.3	129.2	116.1	119.4
$\bar{y}_{.i}$*	115.4	108.8	117.6	118.6	115.1[b]	6.9-13.6[d]
$\bar{y}_{.i}$	112.4	108.4	112.9	121.3	109.8[c]	
			Actual total weaning wt. (g)			
311	266.9	522.5	318.3	630.3	523.7	459.5
312	221.6	587.6	223.5	357.8	267.6	342.6
511	472.1	634.3	651.6	648.0	584.2	601.5
512	440.8	376.8	589.5	628.2	469.0	508.8
$\bar{y}_{.i}$*	378.2	511.2	377.1	545.4	453.0[b]	
$\bar{y}_{.i}$	350.3	530.3	445.7	566.1	533.6[c]	

[a]The terms $\bar{y}_{i.}$ ($\bar{y}_{.i}$) represent the sire (dam) marginal means including the parental lines; $\bar{y}_{i.}$* ($\bar{y}_{.i}$*) are the corresponding means excluding the parental line; parental means are underlined.

[b]Crossbred mean ($\bar{y}_c$).

[c]Parental line mean ($\bar{y}_a$).

[d]Range of subclass standard errors with 16 to 51 observations/subclass.

[e]Adjusted by covariance analysis for linear effects of 21-day litter size.

Table VI.6. Least-squares means for sire by dam subclasses, line of sire and line of dam[a]: cold room.

Sire	Dam 311	312	511	512	$\bar{y}_{i.}$*	$\bar{y}_{i.}$
			21-day progeny body wt. (g)			
311	8.9	9.6	12.4	6.2	9.4	9.3
312	10.8	8.4	11.3	14.4	12.2	11.2
511	12.8	12.3	9.8	12.3	12.5	11.8
512	10.7	10.3	11.3	13.9	10.8	11.6
$\bar{y}_{.i}$*	11.4	10.7	11.7	11.0	11.2[b]	0.3-0.5[d]
$\bar{y}_{.i}$	10.8	10.2	11.2	11.7	10.3[c]	
			Adj. 21-day progeny body wt. (g)[e]			
311	8.9	9.0	12.6	4.9	8.8	8.8
312	10.7	7.8	11.5	14.4	12.2	11.1
511	13.5	12.5	10.5	11.4	12.5	12.0
512	10.3	9.7	11.1	13.9	10.4	11.2
$\bar{y}_{.i}$*	11.5	10.4	11.7	10.2	11.0[b]	1.-2.6[d]
$\bar{y}_{.i}$	10.8	9.7	11.4	11.1	10.3[c]	
			Adj. total weaning wt. (g)[e]			
311	51.6	49.5	70.2	10.0	43.2	45.3
312	63.1	39.9	65.2	81.1	69.8	62.3
511	74.5	70.3	52.5	74.2	73.0	67.9
512	58.0	57.3	64.4	76.9	59.9	64.1
$\bar{y}_{.i}$*	65.2	59.0	66.6	55.1	60.6[b]	6.2-15.4[d]
$\bar{y}_{.i}$	61.8	54.2	63.1	60.6	55.2[c]	
			Actual total weaning wt. (g)			
311	98.8	77.0	124.1	61.6	87.6	90.4
312	140.9	67.6	102.1	242.0	161.9	138.9
511	132.6	200.5	148.4	108.1	147.1	147.4
512	159.4	268.1	397.2	68.7	274.9	223.4
$\bar{y}_{.i}$*	144.3	181.9	207.8	137.5	167.9[b]	
$\bar{y}_{.i}$	132.9	153.3	193.0	120.3	95.9[c]	

[a]The terms $\bar{y}_{i.}$ ($\bar{y}_{.i}$) represent the sire (dam) marginal means including the parental lines; $\bar{y}_{i.}$* ($\bar{y}_{.i}$*) are the corresponding means excluding the parental line; parental means are underlined.

[b]Crossbred mean ($\bar{y}_c$).

[c]Parental line mean ($\bar{y}_a$).

[d]Range of subclass standard errors with 5 to 44 observations/subclass.

[e]Adjusted by covariance analysis for linear effects of 21-day litter size.

In the control room, line 512 had the highest g_{ij} for weaning weight, followed by 312, 511 and 311. In the cold room, the g_{ij} ranking for weaning weights was 511 > 312 > 512 > 311 (Tables VI.5 and VI.6).

Specific Combining Ability. Although the two heaviest progeny groups (511 x 512 and 512 x 512) maintained their position in all analyses, the vast majority of genetic sets ranked differently depending on the presence or absence of covariate(s) in the analysis. When litter size was adjusted to a common mean so that estimates of genetic potential are expressed on an equal basis, the results were quite different than for non-adjusted data.

Reciprocal Crosses. Comparisons on a within environment basis showed that the crossbred progeny from sire lines 312 and 512 to be significantly heavier than the progeny from lines 311 and 511, in the control environment. Crossbred progeny from dam line 312 had significantly ($P < .05$) lighter weaning weights than crossbred progeny from the 3 other dam lines. There were no significant differences in weaning weights of crossbred progeny amongst dam lines 311, 511, and 512 (Table VI.5). Crossbred progeny weaned in the cold environment from line 312 dams were significantly ($P < .05$) lighter than crosses weaned from the other dam lines. Overall, crossbred progeny were 8% heavier than pureline progeny at weaning in the cold environment (Table VI.6).

Both the actual and adjusted (covariate) weaning weights are statistically correct (Tables VI.5 to VI.7) and illustrate the differences in ranking of the specific crosses within each environment and between the two environments. However, the biological meaning will be dealt with in the discussion.

Table VI.7. Least-squares analyses of variance for litter weaning weight, adjusted for litter size, in two environments.

Source	Mean squares			
	d.f.	Control	d.f.	Cold
Sires (S)	3	336.6	3	557.4*
Dam (D)	3	492.4	3	105.8
S x D	9	235.9	9	409.8
Covariate[1]	1	48495.1*	1	17319.6**
Error	50	371.1	21	235.8
Total	67		38	

**P < .01.

*P < .05.

[1]Covariate used in model was litter size.

Table VI.8. General combining abilities (g_{ij}) and maternal effects (m_j) of four lines in two environments for weaning weights.

	Constant estimates for weaning weights	
	Control	Cold
g_{ij} line		
311	-0.74	0.66
312	-0.64	-0.42
511	-0.79	-1.13
512	-2.17	0.88
M_j line		
311	-2.59	-5.12
312	1.63	0.37
511	-2.62	-0.32
512	3.59	5.06

D. Discussion

The environmental effects (i.e. influence of cold temperature) observed in this study were in agreement with Young (1953), Barnett and Manley (1965) and Barnett (1973) for weaning weight and Barnett (1965) for tail length. Heavier dam weights for those rearing litters in the cold environment may have been due in part to increased feed intake. While feed consumption was not measured, observations indicated that feed intake was much greater for mice caged in the cold room. Combining this with the knowledge that lowered external temperature reduces activity, this may partially explain the heavier dam weights. Studies by (Cox *et al.*, 1959 and Carmon, 1963) have shown that males are generally heavier than females at weaning, however, the actual difference in weight due to sex decreased from birth through two weeks and thereafter continues to increase reaching a maximum (males > females by 7%) at 3 weeks of age.

Line of dam was a most influential factor for pre- and post-natal growth traits. Dams from the 512 line produced mice that were consistently heavier at weaning. Crossbred males and females were heavier than purebreds and performed better in each environment than did the purebreds. Carmon (1963) and Kidwell and Howard (1969) reported similar results for crossbreds and purebreds at 21 days of age. Over the combined environments, crossbred averaged 12.60 g compared to 11.76 g for the purebreds. Heterosis for 21-day body weight was significant for mice reared in the cold room (crossbred > purebreds by 8%). In the control rooms crossbreds were approximately 2% heavier than purebreds for 21-day progeny body weights. Thus the effects of heterosis was evident in both environments, but primarily

of consequence in the cold. The one exception to these results was one purebred mating (512) whose progeny performed well (for 21-day body weight) in both environments; this may be partially attributed to their successful response to the pre-evaluation selection for high six-week body weight. Combined with the information that this line was originally from non-inbred stock, which provided it with a larger genetic base for natural selection to act upon, this could account for the success of line 512.

The general combining abilities of the four lines showed that progeny from line 512 ranked highest in both environments for weaning weight. This may be expected because weaning weight has a relatively high heritability and the line had been selected for increased growth rate. Also, maternal effcts could partially account for the better performance of line 512 up to weaning. This was observed for both the selected lines (512 and 312) for weaning weight in both environments.

Hybrid offspring had shorter tails in the control room and much longer tails in the cold room. Does the increased tail length of the crossbred progeny mean that in order to maintain homeostasis in the cold environment, longer tails are needed to get rid of heat? These results indicate that crossbred mice may use their tails as a means of regulating body heat.

Line rankings within each environment were different, indicating the significant effect of environmental temperature on maternal performance from conception to weaning. With regard to the maternal influences in the cold room, these rankings may be partially explained in terms of inbreeding depression of the unselected line 312. All populations had inbreeding levels that had asymptoted to near unity,

but had reached this plateau at different rates because of differnces in population sizes (Fredeen, 1983). Due to the high level of inbreeding and its resultant effect on homozygosity, this line may have lacked the flexibility to perform, being limited to a narrow range of phenotypic expression, and in an unsuitable environment (cold temperature). Carmon (1963) found g_{ij} was significant for 21- and 45-day weight, while Kidwell *et al.* (1960) reported significance for weight at 28 but not at 70 days of age. The performance of reciprocal crosses (r_{ij}) in each environment provides information on any heterotic response in body weight and tail length. Crossbred progeny from dam lines 311, 511, and 512 were superior in weaning weights than other combinations in the cold room. This illustrates that crossbreeding has increased the mean of the sample (for the trait weaning weight) and that additive genes were transmitted to the offspring.

When comparing the performance of a specific cross it is important to keep in mind that the total weight of the litter at weaning (TWW) is the total measurement of female productivity. The line rankings within each environment for TWW were different for almost all combinations, reinforcing the hypothesis that genotypes which are well adapted to one environment may not necessarily be well adapted to a new and different environment.

The assumptions based on the results obtained were in fact limited by the number of mice weaned in each genetic set. The inferences which may be drawn concerning the genetic-environmental interactions are compromised by the lower than expected productivity in the cold environment. It should be noted that the pre-evaluation history of selection was based on first parity data only, a problem common to all experiments where time precludes the use of lifetime records, and this

could influence only extrapolation to lifetime performance. Also, natural selection operating to reduce fertility is certainly a major force in determining the ability of a dam to conceive, bear live, viable pups and wean a healthy litter.

The number of animals weaned per litter is a composite measure of inherent fertility involving the number of ova shed, the number of ova fertilized and the number of offspring counted at birth. The pre- and post-natal death rates are also included in the trait at weaning.

The weight of the litter weaned is even more complex, as it contains in addition to variations due to fertility, number born, birth weight, milk consumed and food eaten by the litter and therefore growth rate before weaning. The actual least squares means for litter weaning weights reflect the effects of treatment on both litter size and individual weaning weight. Whereas, the adjusted least squares means for litter weaning weight represent the effects only on individual weaning weight. Size of dam insofar as it affects maternal performance would also be another variable.

In livestock breeding plans, lines within breeds will be selected for traits which are related to economic importance. In reality, selection for economic traits does improve the genetic merit of the line. However, it is not clear that this same selection procedure will improve crossing ability in another environment. The performance of the various genetic sets in this experiment indicate that productivity (i.e., weaning weight) in different environments will be best achieved by genotypes that have been selected in that environment and are adapted to it. Thus, selection history and adaptation to the environment should be considered in planning animal breeding experiments, particularly for domestic livestock production.

VII. GENERAL SUMMARY AND CONCLUSIONS

The most significant contributions of these experiments with lines of mice selected for body weight on *ad libitum* feeding are summarized below. Responses are examined from a biological rather than from a purely biometrical point of view. Selection for increased body weight in mice usually, though not always, leads to increases in feed intake, growth efficiency and fat deposition, while some aspects of fertility may be impaired.

1. The selected line, HL, was significantly ($P < .01$) heavier than the other lines at both weaning (21 days) and 42 days of age. Males were significantly ($P < .05$) heavier than females within each line.

   Carcass composition results were directly proportional to growth rate. The greatest changes in fat and protein content were found in the line (HL) which had responded greatest to selection for high 42-day weight.

   In the HL line, the contribution of fat to body weight gain was very significant ($P < .01$), even as early as weaning age. Admittedly, the experimental work is deficient because the selected lines were unreplicated. Nevertheless, the HL line showed that selection for rapid growth resulted in a major rise in the contribution of fat to body weight gain. Apart from fat in the HL line, there was little alteration due to selection in the relationships between individual body components and total body weight.

2. If mice are selected to grow faster, it follows that they must do so by eating more, or by utilizing their feed more efficiently, or by some combination of these two. Daily feed intake varied proportionately with growth rate - the fastest growing lines also

consumed the most feed. Analysis of individual feed intake data reveals that the HL consumed more grams of feed throughout the 9 week trial. However, feed eaten (g) per unit body weight gain over the growing period showed the HL line to be more efficient in terms of weight gain, than the other lines. This is presumably related to the relatively higher maintenance requirement of the smaller lines, since they require more feed to maintain one unit of body weight. This is often conventionally explained in terms of higher surface area to mass ratio, with its implications for thermoregulation and its energetic cost. In extrapolating these results to domestic livestock selection for rapid growth, regardless of feed intake level, is this the best direction for future breeding programs? If so, will total fat content come to make up a larger proportion of the total carcass? This question has not been answered, only suggested from the results of selection experiments in poultry and mice.

3. Genotype-environment interactions in the growth rate and reproduction of four different lines of mice reared in two temperature environments were evaluated by a 4x4 diallel cross made within two environments (7 $\pm$ 2°C and 21 $\pm$ 2°). Birth traits recorded were dam parturition weight, litter size and weight, average birth weight and percent mortality. Litter size was unaffected by temperature. Similar litter sizes at birth may have resulted from *ad libitum* feeding and a corresponding greater intake for mice in the cold. Litter weight was lower ($P < .01$) for pups born into the cold environment. Average litter weight (g) in each environment was 14.4 $\pm$ .58 (control) and 11.8 $\pm$ .54 (cold). Percent mortality

was significantly ($P < .01$) higher for offspring born into the cold environment. Minimum effects were due to genetic and heterosis effects at parturition.

4. Litter weaning weight was significantly ($P < .01$) affected by all the main effects (sire, dam, sex, environment) plus sire by dam and sex by environment interactions. Percent mortality was similarly influenced by the main effects (except sex) and to a greater extent by most 2-factor interactions.

Use of covariance analysis to adjust for litter size and dam weight at weaning was done on a within-environment basis. Both covariates were important in the model since they accounted for more of the unexplained variation attributed to error. Total weaning weight of the litter was heavier for mice reared in the control vs cold environment. Within the cold environments the crossbred pups were heavier and had a better survival record than purebred offspring.

The pre-evaluation history of the lines and the level of inbreeding may have accounted for differences observed in the weaning weights of pups raised in different environments. Crossbred progeny showed little gain in body weight (2%) over pureline progeny in the control environment. Crossbred progeny raised in the cold were 8% heavier at weaning than pureline progeny. The heterotic response in weaning weight in the cold environment can be partially explained by the transmission of additive genes to the offspring, allowing them more flexibility in adapting to a different environment.

Livestock species are affected by their thermal environment, the primary effect probably being air temperature. This may result in both physical and psychological complications to the animal's health.

Animals may compensate, within limits, for changes in air temperature by altering feed intake, metabolism and heat dissipation, which in turn alter the partition of dietary energy by the animal. The net result is an altered energetic efficiency, and often an altered reproduction and growth performance.

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